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SC-CAMLR-III/BG/13
3 September, 1984

REVIEW OF ANTARCTIC MARINE FAUNA

Abstract

To aid the development of a better understanding of the ecological relationships and processes in the marine system, a brief overview of the major faunal groups in Antarctic waters (excluding benthos) is provided. The aim is to assist in providing a background against which plans for future research and management programmes may be designed.

Separate sections of the review deal with zooplankton, krill, cephalopods, fish, seabirds, seals and whales. Each section provides information on species composition of particular groups of animals, their geographical distribution and abundance. Where information is sufficient there are descriptions of other biological parameters such as reproduction and growth, food habits and role in the ecosystem.

Krill is considered separately from zooplankton because of its importance as a harvested resource and a prey item for many species in higher trophic levels. The Southern Ocean food web and its trophic relationships are also discussed.

EXAMEN DE LA FAUNE MARINE DE L'ANTARCTIQUE

Résumé

Afin de contribuer à une meilleure compréhension des relations et des mécanismes écologiques dans le système marin, il est donné un bref aperçu des principaux groupes de la faune des eaux antarctiques (à l'exclusion du benthos). Le but en est de fournir un cadre à partir duquel pourraient être conçus de futurs programmes de recherche et d'aménagement.

Le zooplancton, le krill, les céphalopodes, les poissons, les oiseaux de mer, les phoques et les baleines sont examinés dans des sections différentes. Chacune de ces sections comporte des renseignements sur la composition par espèce de certains groupes d'animaux, leur répartition géographique et leur abondance. Lorsque les informations disponibles sont suffisantes, d'autres paramètres biologiques sont décrits tels que la reproduction et la croissance, les habitudes alimentaires et leur rôle dans l'écosystème.

Le krill est considéré séparément du zooplancton étant donné son importance en tant que ressource exploitée d'une part et proie pour de nombreuses espèces dans les niveaux trophiques élevés d'autre part. La chaîne alimentaire de l'océan Austral et ses relations trophiques font également l'objet d'une discussion.

ОБЗОР МОРСКОЙ ФАУНЫ АНТАРКТИКИ

Резюме

Краткий обзор основных групп фауны вод Антарктики (за исключением бентоса) предлагается в помощь достижению лучшего понимания экологических взаимоотношений и процессов в морской системе. Целью является содействие в предоставлении основы для разработки планов будущих исследований и программ управления.

В отдельных разделах обзора содержится информация о зоопланктоне, крилe, головоногих, рыбе, морских птицах, тюленях и китах. В каждом разделе представлена информация о видовом составе определенных групп животных, их географическом распределении и численности. Там, где информации достаточно, даются описания других биологических параметров, таких как вопроизводство и рост, особенности питания и роль в экосистеме.

Криль рассматривается отдельно от зоопланктона в связи с значением его как промыслового запаса и предмета хищничества для многих видов более высоких трофических уровней. Также обсуждается пищевая цепь морей Антарктики и трофические отношения в ней.

REVISION DE LA FAUNA MARINA ANTARTICA

Resumen

Se proporciona una breve revisión de los principales grupos de la fauna en las aguas antárticas (excluyendo el bentos) para asistir en el logro de una mayor comprensión de las relaciones ecológicas en el sistema marino. El objetivo es asistir proporcionando una base sobre la cual se puedan diseñar los planes para una futura investigación y administración.

En secciones separadas de la revisión se trata sobre zooplancton, krill, cefalópodos, peces, aves marinas, focas y ballenas. En cada sección se proporciona información sobre la composición de grupos de animales tomados individualmente, su distribución geográfica y abundancia. En los casos en que se ha obtenido suficiente información, se proporcionan descripciones de otros parámetros biológicos, tales como reproducción y crecimiento, hábitos alimenticios y función en el ecosistema.

Al krill se le considera separadamente del zooplancton debido a su importancia como recurso recolectable y por constituir la presa de muchas especies en niveles tróficos superiores. Asimismo, se trata sobre la cadena alimenticia del Océano Austral y sus relaciones tróficas.

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CHAPTER 1: INTRODUCTION

The Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) recognizes that harvesting living resources could affect the structure and productivity of the Antarctic marine ecosystem. The Convention therefore requires that resource-oriented activities be conducted in such a fashion as to ensure the conservation and maintenance of the Antarctic marine community, including harvested, dependent, and related species.

To be able to pursue enlightened management strategies, it is necessary to develop a better understanding of the ecological relationships and processes in the marine system. To that end, research into the ecology of Antarctic marine fauna is essential. This document's objective is to provide a brief overview of the major faunal groups in Antarctic waters (excluding benthos). Hopefully, this review will assist in providing a background against which plans for future research and management programs may be designed. Bengtson (1984) prepared a report for the U.S. Marine Mammal Commission addressing selected research needs in designing research programs that focus on ecosystem monitoring. This document is the companion paper to that report.

The many persons who generously assisted with the various stages of this review are warmly thanked for their help. Foremost among this group are the four individuals who were the principal authors of the following chapters: M. Burchett, fish; A. Clarke, zooplankton; C. Lockyer, whales; and D. Morris, krill. They did an excellent job of assembling and distilling a large body of literature in a short period of time; any fault in the presentation of the material that they assembled remains my shortcoming. I also wish to acknowledge the following experts who were consulted during the course of this project: D. Ainley, N. Bonner, D. Chapman, J. Croxall, D. DeMaster, I. Everson, R. Laws, S. Mizroch, M. Reinke, D. Siniff, K. Sherman, C. Sullivan, and W. Trivelpiece. Several persons offered their able assistance in reviewing drafts: D. Ainley, D. Chapman, P. Dayton, D. DeMaster, G. Duhamel, R. Hofman, K. Green-Hammond, J. Hureau, G. Joyce, S. McCann, A. North, R. Laws, G.C. Ray, R. Riseborogh, K. Sherman, I. Stirling, and R. Williams. I gratefully acknowledge the office help given by D. Carlquist and N. Carlquist, and I wish to offer special thanks to D. Stinson for her tireless efforts during the entire project. Finally, I thank the staffs of the British Antarctic Survey, the University of Minnesota, and the National Marine Mammal Laboratory for their assistance and forbearance.

CHAPTER 2: ANTARCTIC ZOOPLANKTON

Introduction

The zooplankton present south of the Antarctic Convergence is comprised of a wide variety of taxonomic groups that provides the crucial link between primary producers and carnivores. As noted by Everson (1984a) in his recent review, most attention has been focused on the biology and ecology of Antarctic krill (Euphausia superba*), often overlooking the fact that krill represents but one of the many important taxa. The following paragraphs provide a brief overview of those Antarctic zooplankton species other than Antarctic krill, which is discussed more fully in Chapter 3.

Species Composition

Organisms found in the Southern Ocean include those which can swim actively (nekton) and those which drift with the movements of the water (plankton). The major taxa of Southern Ocean macrozooplankton (those larger than 200 microns) are listed in Table 1. Although the relative abundance of taxa varies with locality and season, in general, the taxa with the largest total biomass are probably copepods, euphausiids, salps, and fish larvae, with cnidarians and pteropod molluscs locally common.

Microzooplankton (smaller than 200 microns) are relatively poorly known, but are the focus of increasing interest because of their importance in the food web (Table 2). A general size classification has frequently been used such as the one of Sieburth et al. (1978):

Megaplankton	20 - 200 cm
Macroplankton	2 - 20 cm
Mesoplankton	0.2 - 20 cm
Microplankton	20 - 200 microns
Nanoplankton	2 - 20 microns
Picoplankton	0.2 - 2 microns

The three larger divisions are often grouped together as plankton, net plankton, or (in a rather loose sense) as macrozooplankton. Picoplankton are sometimes referred to as utraplankton or ultrananoplankton. Although convenient, classifications such as these are only general guidelines to categorizing taxa. Few organisms are of sufficiently regular shape to be classified uniquely into one class or another, and almost no taxa fall entirely within a single size class. Even the fundamental distinction between eukaryote and prokaryote does not classify organisms into any particular size classes.

There are no major groups of zooplankton absent from the Southern Ocean, but the size and relative proportions of various groups differs from zooplankton in the Arctic or the tropics. In most waters of the

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* Throughout all chapters of this paper, the terms "krill" and "Antarctic krill" will refer to Euphausia superba, unless otherwise noted.

Table 1. The dominant taxa of Southern Ocean macrozooplankton. The classification is that of Barnes (1968), with the exception that the Crustacea are considered to be a phylum. Phyla are in capitals, classes in lower case. Synonyms used frequently in the Southern Ocean literature are given in parentheses. References are to the most recent key taxonomic or distributional works.

	Remarks, trivial names, and important species	References
CNIDARIA (COELENTERATA)		
Hydrozoa	Jellyfish-like forms (Hydromedusae). About 66 species. Includes two major divisions: anthomedusae, Sibogita borchgrevinki siphonophores, Diphyes antarctica, and other minor groups.	Totton, 1954; Kramp, 1957; O'Sullivan, 1982d
Scyphozoa	True jellyfish (Scyphomedusae). 11 species. Periphylla hyacinthina, Atolla wyvillei.	Stiasny, 1934; O'Sullivan, 1982c.
CTENOPHORA		
Tentaculata	Comb-jellies or sea-gooseberries. This group has been little studied in the Southern Ocean. Beroe sp., Pleurobrachia sp.	
PLATYHELMINTHES		
Turbellaria	Flatworms. Very little is known of this group in the Southern Ocean.	
NEMERTEA		
Enopla	Ribbon worms. 11 pelagic species of the order Hoplonemertini are known from the Southern Ocean. Pelagonemertes rollestoni.	Wheeler, 1934; O'Sullivan, 1983.
ANNELIDA		
Polychaeta	Segmented worms. About 36 species. Pelagobia longicirrata Tomopteris carpenteri, Vanadis antarctica. The larvae of polychaetes can be important members of the microzooplankton.	Monro, 1930, 1936; O'Sullivan, 1982b
CHAETOGNATHA	Arrow-worms. No classification between genus and phylum has yet been attempted. About 19 species. Ubiquitous in the Southern Ocean. Eukrohnia hamata, Sagitta gazellae.	David, 1955, 1958; O'Sullivan, 1983 Alvarino et al., 1983a, b
MOLLUSCA		
Gastropoda	Pteropods are an important component of the Southern Ocean zooplankton, and are often found in high concentrations. About 31 species. The Southern Ocean fauna includes representatives of two orders: Thecosomata (Eupteropoda; shelled pteropods) Cleodora sulcata, Limacina helea, Spongiobranchia australis Gymnosomata (Pterota; shell-less pteropods) Clione antarctica Molluscan larvae also occur in the microzooplankton.	Massy, 1932
CRUSTACEA	The crustaceans are probably the most important taxonomic group in the Southern Ocean.	
Amphipoda	Hyperoche medusarum, Parathemisto gaudichaudii	Barnard, 1932; Holman and Watling, 1983.
Copepoda	Calanus acutus, C. propinquus, C. simillimus, Clausocalanus laticeps, Ctenocalanus vanus, Derpanopus pectinatus, Euchaeta antarctica, Metridia gerlachei, M. lucens, Pleuromamma robusta.	Vervoort, 1965; Bjornberg, 1967; Heron, 1977; Park, 1978, 1980, 1982, 1983a, b.

Table 1. Continued.

Decapoda	Rarely found at the surface, but a dominant group in the midwater fauna, as in other oceans. Pasiphaea scotiae, Hymenodora glacialis.	Yaldwyn, 1965; Kirkwood, in press.
Euphausiacea	Euphausia crystallorophias, E. frigida, E. superba, E. triacantha, E. vallentini, Thysanoessa macrura, T. vicina.	John, 1937; Baker, 1959; Marr, 1962; Kirkwood, 1982.
Isopoda	This largely benthic group is a minor component of the Southern Ocean zooplankton.	Schultz, 1978
Mysidacea	Antarctomysis maxima, A. ohlini.	Tattersall, 1955
Ostracoda	As in other oceans, a small but ubiquitous component of the Southern Ocean zooplankton. About 17 species south of 60°S.	Deevey, 1978, 1982
	Crustacean larvae (including larvae of benthic forms such as cirripedes) are also important in the microzooplankton.	
ECHINODERMATA	No adult echinoderms occur in the plankton, but the large larval form Auricularia antarctica is frequently common in the macrozooplankton. Other echinoderm larvae also occur in the microzooplankton.	
CHORDATA		
Thaliacea	Salps. Important members of the Southern Ocean plankton, which can be present in vast numbers in summer. Salpa thompsoni (formerly S. fusiformis var aspera), S. gerlachei.	Foxton, 1961, 1966; O'Sullivan, in press.
Osteichthyes	Larval fish can be very important members of the plankton at certain times of the year.	

Table 2. Southern Ocean zooplankton smaller than 200 microns (microzooplankton, nanoplankton, picoplankton). The eukaryote protist classification is that of Margulis and Schwartz (1982).

Taxon	Synonyms, trivial names and representative Antarctic genera	Remarks
PROKARYOTES	Bacteria	Abundant; autotrophic and heterotrophic.
EUKARYOTE PROTISTS -		
Bacillariophyta	(Bacillariophyceae). Diatoms; Chaetoceros, Nitzschia, Corethron, Thalassiothrix.	Abundant; exclusively photo-autotrophic.
Haptophyta	(Prymnophyceae). Includes coccolithophorids. Phaeocystis.	Abundant; can be flagellated.
Dinoflagellata	(Dinophyceae). Dinoflagellates. Protoperidinum.	Abundant; Flagellate; both photo-autotrophic and heterotrophic.
Chrysophyta	(Chrysophyceae). Includes silicoflagellates. Distephanus.	Flagellate.
Chlorophyta	(Prasinophyceae).	Flagellate.
Euglenophyta		Flagellate; both photo-autotrophic and heterotrophic.
Zoomastigina	Includes choanoflagellates and bicoecids. Parvicorbicula.	Abundant; flagellate; heterotrophic (especially consumers of bacteria).
Foraminifera	Globigerina	Abundant.
Ciliophora	Ciliate protozoa. Includes tintinnids.	Abundant.
Actinopoda	Includes radiolarians	
METAZOA		
Rotifera		
larvae of	Echinodermata Mollusca Crustacea Polychaeta	These larvae are occasionally abundant, but the tendency for benthic species to produce large eggs which are then brooded, means that the Southern Ocean zooplankton is poor in larvae compared with other oceans.

world, copepods are the major zooplankton herbivores, whereas in the Antarctic the euphausiids (notably E. superba), and sometimes salps, are dominant. The reason for this difference is not understood, but it is possible that the evolution of a very large euphausiid (E. superba), which not only competes for food with copepods but possibly also preys on them, has shifted the balance of community structure. The evolution of several species of large zooplankton in the Southern Ocean may be related to ecological conditions such as a relatively stable temperature regime and a distinctly seasonal primary productivity. Certainly a tendency towards the evolution of large species is shown by Antarctic benthos (see Clarke, 1979).

The size of zooplankton may also be controlled by the impact of plankton-eating fish. Where these predominate, zooplankton will be small (copepods); but where such fish are less abundant, large planktonic herbivores can evolve (Koslow, 1983). The general lack of truly pelagic Antarctic fish may be a factor in allowing the evolution of a dominant, large, zooplankton herbivore. Interestingly, in the Weddell Sea and Ross Sea areas, where there are large schools of the Nototheniid fish Pleurogramma antarcticum (DeWitt, 1970), the zooplankton is dominated by groups other than euphausiids. Euphausiids do occur in these areas, and they are the dominant prey taken by P. antarcticum (DeWitt and Hopkins, 1977).

Distribution

Although the Antarctic Convergence is generally considered the northern boundary of Antarctic waters, many zooplankton species are found both north and south of this front. Examples include Parathemisto gaudichaudii (one of very few truly bipolar species), Euphausia triacantha, and Limacina balea. The Convergence apparently does constitute a northern barrier for species such as Euphausia superba and Salpa thompsoni. The Sub-tropical Convergence appears to be a much stronger faunal barrier (Peres, 1982), with both physical and chemical oceanographic features suggesting that it is a more important barrier to zooplankton than the Antarctic Convergence.

Baker (1954) analyzed the distribution of 38 species of the more common Southern Ocean macrozooplanton and found that, with the possible exception of the amphipod Eusirus antarcticus, all were circumpolar. This pattern is most likely related to the predominantly circumpolar flow of the superficial water masses. Foxton (1956) detected no significant variation in the zooplankton volume found in the water column (0-1000 m) around the Antarctic continent.

Thermal segregation

A north-south cline in species composition is a general component of Antarctic zooplankton distribution. The euphausiids are a good example of this pattern (John, 1937). From an analysis of zooplankton taken in the Bransfield Strait, Scotia Sea, and South Georgia area, Mackintosh

(1934) divided the various species into a series of groups based on temperature preferences. This classification has been summarized recently by Everson (1984a):

Warm water species

1. Species confined to water above 3°C: Euphausia vallentini.

2. Typical warm water species: Calanus simillimus, Candacia sp., Eucalanus sp., Heterorhabdus sp., Pleuromamma robusta (copepods), Euphausia triacantha.

3. Warm water species also found in colder water: Limacina balea (pteropod), Euchaeta sp. (copepod), Parathemisto gaudichaudii (amphipod), Euphausia frigida.

Widespread species

4. Species with wide temperature tolerance, but with a slight preference for warmer waters: Rhincalanus gigas (copepod), Spongiobranchia australis (pteropod), Primno macropa (amphipod), Thysanoessa sp. (euphausiid).

5. Neutral species: Haloptilus sp., Euchirella sp. (copepods), Cyllopus sp. (amphipod), Solmundella sp. (hydrozoan).

6. Species with wide temperature tolerance, but with a slight preference for colder waters: Calanoides acutus, Calanus propinquus (copepods), Vibilia antarctica (amphipod).

Cold water species

7. Cold water species found in large numbers anywhere south of the 3°C isotherm: Euphausia superba, Salpa thompsoni, Tompteris sp. (polychaete), Metridia gerlachei (copepod), Cleodora sulcata, Clione antarctica, Limacina helincina (pteropods), Pyrostephos vanhoffeni (siphonophore).

8. Species typical of the coldest regions, rarely or never approaching the Antarctic Convergence (except around South Georgia): Sibogita borchgrevinki (anthomedusan), Diphyes antarctica (siphonophore), Eusirus antarcticus, Haloptilus ocellatus (copepods), Vanadis antarctica (polychaete).

Neritic species

9. Euphausia crystallorophias, Antarctomysis maxima.

Hempel (1984) suggested that Southern Ocean zooplankton can be viewed simplistically as three concentric rings. The outer ring corresponds to the West Wind Drift, and is a region dominated by copepods (the localized

concentration of Euphausia superba around South Georgia is an exception to this generalization). Further south is a ring corresponding roughly to the East Wind Drift and its associated fronts. This area is dominated by euphausiids (principally E. superba) and salps, and is the zone of strong seasonal variation in pack-ice cover. The third zone is adjacent to the Antarctic Continent itself, and comprises principally the Weddell Sea and Ross Sea. Here ice cover is substantial, and preliminary studies indicate that the major zooplankton groups are siphonophores and pteropods; euphausiids and salps evidently are rare here.

Not all Antarctic zooplankton species are circumpolar. Foxton (1966) noted that the salp Salpa thompsoni is found in all sectors of the Southern Ocean and as far north as the Sub-tropical Convergence. It is found only infrequently close to the Antarctic continent, and appears to be absent from the Weddell Sea. The similar species S. gerlachei, however, is found almost exclusively south of 65°S, and only in the Pacific sector (roughly 70°E to 180°E). Caldwell (1966) found broadly similar distributions, though S. gergachei was reported from 60°E, suggesting the possibility of transport through the Drake Passage to the Atlantic sector.

Swarming

Although swarming behavior is a noticeable feature of several important Southern Ocean zooplankton species, the function of swarms is not always clear. It is highly likely, however, that the mechanism of swarming is different in different species. Foxton (1966) showed that swarms of Salpa thompsoni were present in summer when abundant food led to rapid proliferation of individuals by asexual budding. A swarm of salps may therefore represent nothing more than many individuals close together because reproductive conditions are good. The swarming of krill appears to be an active process perhaps related to feeding, reproduction, or predator avoidance (a parallel is frequently drawn between the swarming of krill and the schooling of small fish). Other organisms which form swarms or occur in dense concentrations include the amphipods (e.g., Parathemisto gaudichaudii) and pteropods.

Vertical migration

Two aspects characterize the vertical distribution of zooplankton in the Southern Ocean: 1) a so-called diurnal vertical migration, and 2) a seasonal change in the depth. Vertical migration of Antarctic zooplankton has been studied most intensively in Euphausia superba. Other euphausiids also undertake vertical migrations (e.g., E. frigida, E. triacantha), as do Salpa thompsoni and the copepod Pleuromamma robusta (Mackintosh, 1937). Little is known of the reasons for vertical migration (or the lack of it in the many species which show no marked circadian rhythm of depth). The complex patterns exhibited by E. superba, however, indicate that it is not simply a balance between the competing effects of food requirements and predator avoidance (Iwasa, 1982). Because the variation in temperature of the Southern Ocean with

depth is relatively small, it seems unlikely that organisms could gain much energetic benefit from resting at depths as proposed by McLaren (1963, 1974) as influencing the evolution of vertical migration.

A detailed consideration of the seasonal vertical migration of copepods in the Pacific sector of the Southern Ocean was provided by Hopkins (1971). In winter (roughly May to August) less than 10% of the total biomass of 4 species (Rhincalanus gigas, Calanoides acutus, Calanus propiquus, Metridia gerlachei) was present in the top 250 m of the water column. From September onwards copepods migrated into these surface waters, arriving sequentially by species. Voronina (1972) found that in spring when Calanoides acutus is found exclusively in the surface layers, Rhincalanus gigas is still at depth. Calanus propinquus is the next species to rise, followed by Rhincalanus gigas. There is a similar timing for descent into deeper waters (Voronina, 1975).

Other species which spend the summer months in the surface layers and the winter in deeper water are Eukrohnia hamata, Sagitta gazellae (David, 1955, 1958, 1965), and Salpa thompsoni (Foxton (1966). This list includes both herbivores and carnivores, and Foxton (1964) noted that the maximum standing stocks of the predatory Sagitta gazellae occurs later than that of herbivores such as Calanoides acutus.

Control of distribution

Although the general distribution of the major zooplankton species are known, so little is known of the biology of most species that ideas regarding the factors controlling distribution are little more than speculation. It has long been realized that a seasonal vertical migration from the southerly moving Warm Deep Water into surface waters with a strong northerly component would maintain organisms within broad latitudinal bands (Mackintosh, 1937). Such a mechanism might also work on a daily basis, though obviously on a much smaller scale. Some larger organisms (for example E. superba and salps) are capable of sustained, active swimming and seem likely to be able to maintain their geographical position against prevailing water movements.

Abundance

Estimates of zooplankton biomass (other than E. superba) derive almost exclusively from net haul data. Unfortunately, the large range of physical size, activity (and ability to avoid sampling gear), biology (notably patchiness), and absolute density present enormous difficulty in making reliable estimates of biomass. Large species such as medusae and salps are frequently excluded from estimates based on net-hauls because of these organisms' size and relatively low frequency of occurrence, which give them an unrealistic weighting in statistical analyses (Everson, 1984a). Nevertheless, in summer salps can constitute a major portion of the zooplankton biomass in some areas; if salps and cnidarians are included in biomass estimates, these can outweigh all other groups. For example, Hardy and Gunther (1935) list the number of individuals of

Table 3. Percentage of total biomass for the major taxa of Southern Ocean zooplankton - not detected. *, found but not quantified. **, found but weight included in figure for other taxa. All data % total biomass (wet wt).

	Voronina and Naumov 1968 0-500 m		Maruyama et al., 1982 300 m		Hopkins, 1971 0-1000 m	Williams et al., 1983 0 - 400 m	
	Sub Ant.	Ant.	61-65°S 122-125°E mean of 7 stns	65°S 166°S stn 103	Pacific Sector	60°-67°	60-90°E Indian Ocean Sector
	Indian Ocean Sector						
Medusae	2.1	3.6	*	*	*	6.1	25.1
Siphonophores			*	*	*	4.5	1.1
Ctenophores	*	*	*	*	*	1.7	0.3
Polychaetes	1.5	1.3	3.3	-	**	0.9	1.3
Chaetognaths	13.2	9.8	15.5	11.5	10.0	3.1	0.5
Pteropods	2.4	0.9	1.9	0.9	**	4.0	1.1
Amphipods	*	*	7.8	5.1	**	3.4	0.9
Copepods	61.5	72.8	63.3	35..0	48.8	10.9	0.4
Euphausiids	7.2	7.6	8.0	47.0	7.5	57.0	66.8
Salps	4.9	0.9	*	*	*	4.4	1.2
Other taxa	7.2	3.1	0.2	0.5	33.7	4.0	1.3

the 6 major zooplankton species taken at night around South Georgia (their Table 62, p. 316). Catches of E. superba varied from 0 to 42,500 individuals, and catches of Salpa thompsoni from 2 to 10,835. The ratio of Salpa to E. superba numbers ranged from 63 to 0.0012 (ignoring all instances where no krill were caught). The high wet weight biomass of salps and their very patchy distribution presents a difficult statistical problem, since they are undoubtedly important organisms in the Southern Ocean. To exclude them from calculations may bias the results just as much as including them. Gelatinous zooplankton cannot, however, just be ignored (as is often done). They include both predatory and herbivorous forms, and their impact on phytoplankton and zooplankton stocks is very likely to be high. Some means of measuring their patchy distribution must be developed or our understanding of Southern Ocean zooplankton biomass will remain flawed.

Another problem in making biomass estimates from net hauls is that of net bias and net avoidance. This difficulty is well shown by the FIBEX (of the BIOMASS program) catch data for the Indian Ocean Sector. Samples were taken mostly between 60°S and 66°S; those taken with Bongo nets contained 6% medusae, 11% copepods, and 57% euphausiids (by weight). Those taken with the RMT8 (blind hauls, no deep hauls included) averaged 25% medusae, less than 1% copepods, and 67% euphausiids (Williams et al., 1983). Coupled with natural patchiness, such sampling variation can lead to vast differences in sample composition from area to area. For example, the three different survey blocks in the FIBEX Bransfield Strait Area A contained 41, 16, and 41 g/m^2 of zooplankton (Rakusa-Suszczewski, 1983).

Some recent estimates of the relative importance of various taxa are summarized in Table 3. It is clear that the major zooplankton taxa in the Southern Ocean are copepods and euphausiids, in that order. Few data, however, are available for areas presumed to be dominated by krill; most biomass estimates come from areas known to be dominated by copepods rather than euphausiids.

Table 4 presents various estimates of total zooplankton biomass. Using the reasonable median value of 50 mg/m^3 (wet weight) for zooplankton biomass in the top 1000 m suggested by Everson (1977), and assuming the area of the Southern Ocean to be 36 million km^2 produces an estimated 'total' zooplankton biomass of 1800 million tons (wet weight). This figure excludes Euphausia superba, fish, and gelatinous zooplankton (salps, ctenophores, and medusae). At present, there is no reliable way of estimating this missing biomass, and because of the wide variability of the estimates figures for zooplankton biomass must be treated with caution (Everson, 1984a).

Zooplankton biomass is not distributed evenly in the Southern Ocean. Foxton (1956) showed that from the equator to about 30°S, zooplankton biomass was relatively constant and low. Around 50° - 55°S near the Antarctic Convergence biomass increased by up to seven fold. Closer to the Antarctic continent, biomass decreased somewhat, but remained high in

Table 4. Estimates of the standing stock biomass (wet weight) of Southern Ocean macrozooplankton. Table modified from Everson (1977). *data presented as displacement volume, recalculated assuming 1 ml = 1 gram wet weight. **data presented as dry weight, recalculated assuming dry weight = 20% wet weight.

Standing stock biomass	Depth range (m)	Notes
Volume basis (mg/m^3)		
23-43*	0-250	Subantarctic waters; Foxton, 1956 recalculated by Maruyama et al., 1982.
55*	0-50	Southern Ocean mean; Foxton, 1956 recalculated by Everson, 1977.
25-37*	0-250	Southern Ocean mean; Foxton, 1956 recalculated by Maruyama et al., 1982.
6-25*	0-1000	Southern Ocean mean; Foxton, 1946 recalculated by Everson, 1977.
		All the above data exclude Euphausia superba, salps, medusae and fish.
1000-2000	0-50	Feb/March, close to shore ice;
100-150	100-200	Vinogradov and Naumov, 1958, (in Everson 1977).
50	200-500	
10-100	0-500	20°E to 160°E; Voronina, 1966 (in Maruyama et al., 1982). Includes salps and medusae.
100	?	Around 60°S; Bogorov et al., 1968 (in Everson, 1977).
27-53**	?	155°E to 155°W, rich area;
5-27**	?	155°E to 155°W, intermediate area;
<5	?	155°E to 155°W, poor area; all data from Barkhatov et al., 1973 recalculated by Maruyama et al., 1982.
560±200*	0-100	Between sub-tropical and Antarctic convergences;
120±170*	0-100	South of the Antarctic Convergence;
760-110*	0-100	In regions of maximum phytoplankton abundance; Voronina and Zadorina, 1974.
29-31	0-370	120°E to 170°E; rich areas;
14-20	0-370	poor areas; Maruyama et al., 1982. Zooplankton retained by 1 mm mesh; excludes medusae and salps.
Area basis (g/m^2)		
13.5**	0-1000	Antarctic; Pacific sector of West Wind Drift;
15.0**	0-1000	Antarctic Convergence zone; Pacific sector;
13.0**	0-1000	Between Subtropical and Antarctic Convergences; zooplankton retained by 0.2 mm mesh; Hopkins, 1971. Excludes medusae, siphonophores, foraminifera and radiolaria.

comparison with tropical and sub-tropical waters.

A similar comparative study by Hopkins (1971) revealed less extreme variation. Total zooplankton standing crop in the top 1000 meters of the Pacific sector was 2.67 g/m^2 (dry weight) in the Antarctic zone, 2.96 g/m^2 at the Antarctic Convergence, and 2.58 g/m^2 between the Antarctic and Sub-tropical Convergences. These figures are only moderately higher than other oceans of the world, although they do confirm the increase in zooplankton biomass around the Antarctic Convergence. This increase is also evident in the map of zooplankton biomass given by Peres (1982), based on Vinogradov and Naumov (1961).

Little is known of the productivity of Southern Ocean zooplankton. Peres (1982) estimated an annual production of 190 - 380 million tons (wet wt) for all zooplankton in the Southern Ocean excluding krill. The latter was estimated at 95 - 190 million tons per annum from biomass data, and at 130 - 1000 million tons per annum from primary production data. Thus estimated production of zooplankton other than krill, expressed as a fraction of total production, is either 67%, or 28 - 59%, depending on the method of estimating krill production.

Southern Ocean secondary production was estimated in a series of papers (Voronina et al., 1979a, 1980a, b, c). These studies considered the life cycles of the three dominant copepods Calanoides acutus, Calanus propinquus, and Rhincalanus gigas. Their distributions were divided into northern, intermediate, and southern zones to allow for a seasonal cline in distribution (Table 5).

When the total annual production of 54.8 g/m^2 is added to molting and nauplii biomass, total annual net production comes to 62.0 g/m^2. Including euphausiids (biomass from net hauls 1.9 g/m^2, annual P/B ratio 2.38) increases production by 4.5, to 66 g/m^2. Adding all other zooplankton brings the total annual net zooplankton production to 70 g/m^2. This estimate includes 88.6% copepods, 6.4% euphausiids, 5% other, and gives a total estimate of Southern Ocean secondary production of 2520 million tons (wet wt) per annum. Excluding euphausiids only reduces the estimate to 2360 million tons per annum. Hence, euphausiid production is a relatively small fraction of total secondary production.

Growth and Reproduction

A broad variety of life history strategies have evolved among Antarctic zooplankton (Table 6). The life-history of the copepod Calanoides acutus is somewhat typical for herbivores (Andrews, 1966). In winter the population is at depth, and consists almost entirely of stage IV and V copepodids. These do not feed, but live off reserves stored as a wax droplet. Reserves are at a maximum in April/May, and decline throughout the winter. In October and November these immature animals molt to become adults, mate, and rise to the surface to feed on phytoplankton (primarily diatoms, as indicated by gut contents). December and January are the periods of peak egg production, and the emergent nauplii rapidly grow to stage III and IV copepodids by late

Table 5. Annual production and production/biomass values for three species of Antarctic copepods. (After Voronina et al., 1979b, 1980 a, b, c, d).

Species	Total annual production in grams (wet wt) per m^2	Annual P/B ratio
Rhinocalanus gigas	28.4	5.3
Calnoides acutus	18.1	4.5
Calanus propinquus	8.3	-
Total	54.8	

Table 6. A summary of published ecological studies of Southern Ocean zooplankton.

Species	Major features of the life-history
CHAETOGNATHA	
Sagitta gazellae	Carnivorous, eating mainly copepods and euphausiids. Grows throughout the year, although faster in summer. Achieves sexual maturity in about 1 year. Spawns in all months, though mostly in summer. Small eggs released directly into the sea. Seasonal vertical migration by bulk of the population. (David, 1955, 1965)
CRUSTACEA	
Amphipoda	
Parathemisto gaudichaudii	Two morphs: long-legged (bispinosa), and short-legged (compressa) forms. Voracious carnivore. Winter population mostly immatures, although by August 80% are mature. Females brood batch of eggs, and produce several broods per summer. Spawning mainly September-December, but can extend further towards autumn. Little growth over winter, and life-cycle probably lasts only one year in most individuals. (Kane, 1966)
Copepoda	
Calanoides acutus	Herbivorous. Overwinters without feeding in deep water as stage IV and V copepodids, utilising wax reserves in droplet. Moult to stage VI adults, and rise to feed in surface waters in October/November, when almost all females carry sperm sacs. Ready to spawn in November, and peak egg production in December and January. Early copepodid stages feed on bloom, mature to stage III or IV with full wax droplet, and descend to overwinter at depth. Presence of two peaks of stage VI adults suggests possibility that eggs spawned early may mature to adults within one summer. Alternatively autumn spawning in higher latitudes may merely reflect later timing of whole life-history to match development of ice-edge bloom. Life-cycle probably takes one year. (Andrews, 1966; Voronina, 1968)
Rhincalanus gigas	Herbivorous. Overwinters without feeding in deep water as Stage IV and V copepodids. State of maturity in spring depends on water temperature. Around South Georgia, mature in surface waters in late November/December. Spawns in December around South Georgia, later in colder waters further south (January in Weddell Sea). However also possibility that the eggs of early spawners in warmer northern waters may mature in one season, spawning themselves in deep warm water in May/June. Life-cycle probably takes one year. (Ommanney, 1936)
Euphausiacea	
Euphausia superba	Probably omnivorous, though taking much phytoplankton in summer. Growth probably confined to summer; possibility of shrinkage in winter confuses size/frequency histograms. Life-cycle probably more than 2, possibly 4 years. Spawns in mid-summer; ovary matures rapidly and extended spawning period. (Marr, 1962; Everson, in press)
Euphausia triacantha	Probably omnivorous. Grows throughout the year, but more quickly in summer. Spawns in spring (the ovary having matured during the previous winter). Life-cycle takes about two years. (Baker, 1959a

Table 6. Continued

Mysidacea	
Antarctomysis maxima	Probably omnivorous. Growth rapid in summer, growth rate in winter unknown but possibly similar to Euphausia triacantha. Spawns in 2nd summer at South Georgia, brooding eggs over the winter, and releasing these next spring. Maturity reached after 3 or 4 years further south (South Orkneys), and brood size reduced though eggs are larger. (Ward, in press)
CHORDATA	
Thaliacea	
Salpa thompsoni	Herbivore. Diurnal migration, and marked seasonal vertical migration. Winters in deep water, where growth is slow (6-8 mm/month), and there are no large individuals in the population. Rise to surface in summer, when growth is rapid. Frequent asexual budding leads to high numbers, colonial forms, and large individuals. Life-cycle probably about one year. (Foxton, 1966)

summer (March/April). With a full wax droplet they then migrate downwards to overwinter. Growth and reproduction are thus clearly limited to summer; winter is spent without feeding as CIV and CV stages. The complete life-cycle takes one year. A similar pattern is shown by the dominant copepod of the West Wind Drift, Rhincalanus gigas (Ommanney, 1936). In both Calanoides and Rhincalanus, the production of eggs and larvae is synchronous with the phytoplankton bloom. The breeding season is thus later in higher latitudes, and the timing of the life-cycle follows the retreat of the melting ice-front (Voronina, 1968).

A somewhat different physiological strategy is followed by the salp Salpa thompsoni (Foxton, 1966). As with Calanoides acutus, the population winters at depth, but individuals do grow slowly. There are no apparent lipid reserves for overwintering, but these are difficult to distinguish in gelatinous zooplankton and may not have been accurately reported (Clarke, in press a). Perhaps the generalist feeding method of salps allows them to obtain some energy in winter. In summer salps migrate to surface waters where growth and reproduction proceed rapidly. Because salps reproduce both asexually (budding) and sexually, the processes of growth and reproduction are partly indistinguishable.

One of the few studies of a fully carnivorous species of Southern Ocean zooplankton is that by David (1955) of the chaetognath Sagitta gazellae. This species apparently feeds year-round. Growth continues during winter (at about 5 mm/month from May to November) and there is no major lipid reserve (Clarke, in press b). Growth is probably more rapid in summer, but the mixture of age classes and the possibility of body-shrinkage during periods without food (Reeve et al., 1970) mean that interpretation of size/frequency histograms is difficult. Reproduction occurs throughout the year (though mostly in summer), and sexual maturity is probably reached in about 12 months.

Like most euphausiids, Euphausia triacantha is omnivorous. It takes about two years to mature, and growth continues throughout the year, although the rate slows somewhat in winter (Baker, 1959a). Its eggs are spawned in spring, allowing newly emergent larvae to feed on summer phytoplankton bloom. Lipid reserves are moderate, and are divided roughly evenly between wax ester and triacylglycerol (Clarke, in press b), which suggests a partial reliance on lipid for overwintering.

Antarctomysis maxima develops an ovary during the summer, spawns, and broods the eggs over winter. The eggs hatch the following spring. Females probably mature within two years at South Georgia, but take longer at higher latitudes (Ward, in press). The amphipod Parathemisto gaudichaudii also broods its eggs, but completes its life cycle in about one year (Kane, 1966). Again, the timing of larval release coincides with the spring phytoplankton bloom; both species store wax ester as well as triacylglycerol.

The wide divergence of life history strategies observed in Southern Ocean zooplankton indicates that there is no single answer to the

problems posed by living in a cold, seasonally productive environment. Some species have short life-spans, others long; some species grow year-round, others only in summer; some brood their eggs, others spawn directly into the sea. Nevertheless, there is evidently a trend for overall growth rates to be slow, longevity to be increased, and population turnover to be slow. Although the data for zooplankton are sparse, the tendency is very clearly marked among the errant benthos (A. Clarke, 1983). This tendency is sometimes termed K-strategy, and is expected when major environmental variables are seasonal but predictable (see Clarke, 1979).

Food Habits

If it is accepted that many species classed as herbivores may also feed to some extent on heterotrophic micro-organisms, then the major division of trophic modes in the zooplankton are:

1) herbivores feeding by filtration, also taking microzooplankton or bacterioplankton (e.g., calanoid copepods, small euphausiids, and salps), and

2) carnivores/omnivores, feeding on larger particles or organisms (e.g., larger euphausiids, euchaetid copepods, arrow-worms, amphipods, polychaetes, pteropods, and larval fish).

Although the herbivore/carnivore ratio varies seasonally and by area, herbivores usually outweigh carnivores (Hopkins, 1971).

An important biological and physiological difference between these two modes of nutrition lies in the seasonal availability of food. Although data are scarce, it appears that very low quantities of small particulate matter are present in the water column during winter. Therefore, most herbivorous species are without food, and must rely on lipid reserves synthesized the previous summer (Clarke, in press b). These lipid reserves can be large and are frequently composed of wax ester, as shown by calanoid copepods. In contrast, omnivorous or carnivorous zooplankton can maintain low levels of feeding during winter, hence avoiding a need for a lipid store (Clarke, in press b).

The Southern Ocean Food Web

A traditional explanation for energy pathways in the Southern Ocean has been linear:

phytoplankton (diatoms) ⇨ *E. superba* ⇨ krill consumers

It is now increasingly clear that the Antarctic marine system is much more complex. Antarctic krill, although certainly of major importance ecologically and commercially, may not be as absolutely pivotal as previously thought. Changes in our understanding of interactions between marine organisms have taken place throughout the Southern Ocean food web. We now know that autotrophic production is by no means limited to diatoms and dinoflagellates; it is likely that there is a complex bacterial/microzooplankton community important in grazing and

remineralization; there is substantial input to the system from the ice-associated flora and fauna; and other macrozooplankton herbivores (most notably copepods and salps) are at least as important ecologically, and perhaps more important than krill in some areas (Clarke, in press b). A speculative food web for the Southern Ocean, incorporating some of these changes in emphasis, is shown in Figure 1.

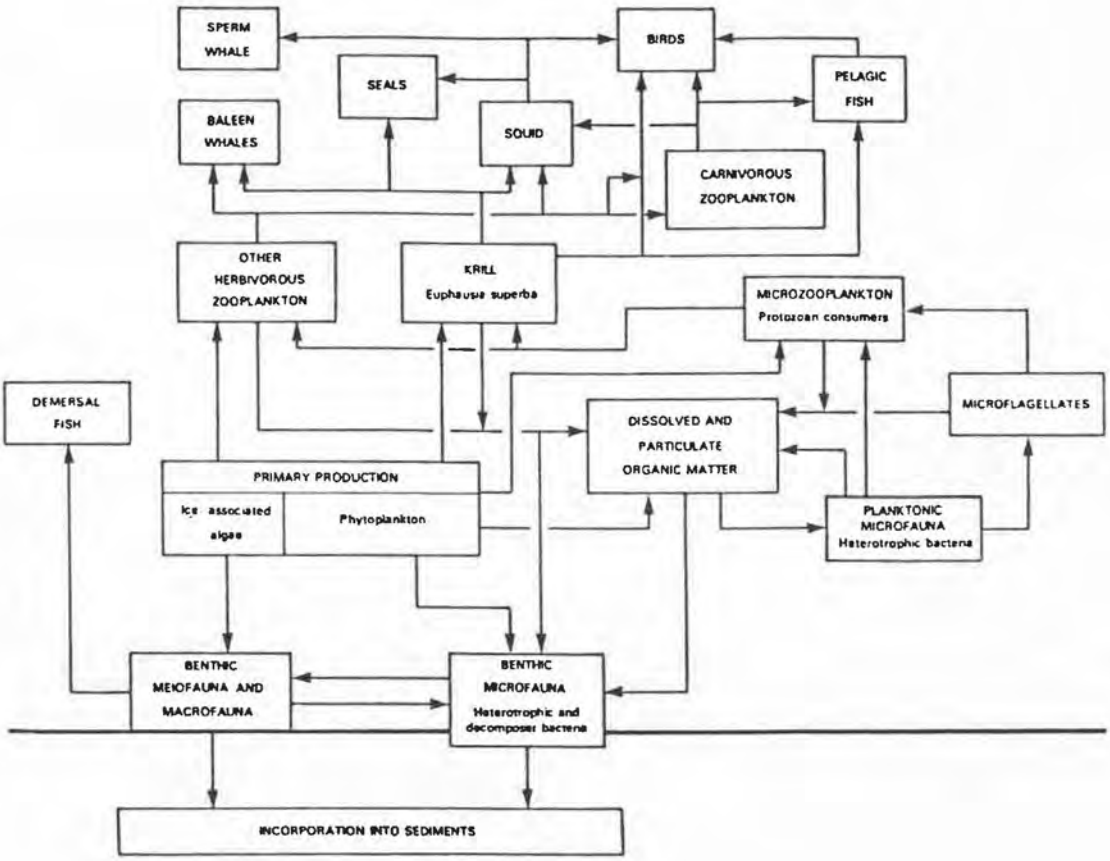
Primary production

Southern Ocean primary production varies widely between sites (Whitaker, 1982). Recent studies have shown that in addition to diatoms, groups such as dinoflagellates, silicoflagellates, and several other autotrophic organisms are present in the Southern Ocean (Buck and Garrison, 1983). Significant primary production occurs in tropical waters in very small photosynthetic eukaryotes (Li et al., 1983). The discovery of flagellates smaller than 3 microns in Weddell Sea waters (Buck and Garrison, 1983) suggests that these organisms may also be significant in the Antarctic. Because many of these organisms pass through the filters routinely used in the determination of ^{14}C-fixation, primary productivity may have been underestimated.

There have been several attempts to estimate total open-ocean annual primary production in waters south of the Antarctic Convergence (summarized in Everson, 1977). A frequently quoted figure is 6400 million tons (wet weight) per annum (Holm-Hansen et al., 1977). This figure, however, is derived from ^{14}C- fixation data obtained in open waters. It is likely that production by very small autotrophs may have been missed (see von Brockel, 1981). In addition, such estimates may fail to account for carbon fixation by ice-associated algae. Sea-ice can contain a very high biomass of phytoplankton, most of which is released as the sea-ice melts. The quantitative importance of this phenomenon is as yet undetermined, but studies in both the Arctic and Antarctic have shown that intense blooms develop in the wake of the melting ice front (Horner, 1976; Niebauer et al., 1981). Studies of dynamics of the pack ice ecosystem are currently underway (e.g., AMERIEZ program in U.S.).

Obtaining reliable estimates of the Southern Ocean primary productivity remains a challenge. Foxton (1956) and Hopkins (1971) demonstrated a high zooplankton biomass in the Southern Ocean which must be supported by a high annual plant production. It is reasonable to conclude that a large zooplankton biomass growing and producing gametes in summer requires a large input of energy from food. The potential problem that data for open-ocean carbon fixation may be too low leads to the assumption that the Southern Ocean is no more productive than elsewhere (despite evidence of high zooplankton biomass). Perhaps the paradox will be resolved when better quantitative estimates of production by picoplankton (common to all oceans) and ice-associated algae (unique to polar regions) become availale.

Fig. 1. A proposed food web for the Southern Ocean. (From Clarke, in press a).



Dissolved organic matter, microheterotrophs, and the microzooplankton

The fate of fixed carbon in the Southern Ocean is poorly understood, but studies from other seas suggest that a sizeable fraction enters the pool of dissolved organic carbon where it is utilized by heterotrophic bacteria. The proportion of fixed carbon released by phytoplankton varies widely between 1 to 69.7% from different areas (none polar) (Joint and Morris, 1982). Nutrient status is an important factor in governing this release, and modern techniques of estimating microbial biomass and production have shown that the marine microbial fauna is intimately linked to phytoplankton biomass. Dissolved organic carbon is also utilized by heterotrophic microflagellates (see Azam et al., 1983; Linley et al., 1983). Very little is known about Southern Ocean dissolved organic carbon or bacteria, although open ocean heterotrophic bacterial activity appears to be comparable with other areas of the world (Morita et al., 1977; Bolter and Dawson, 1982). Fuhrman and Azam (1980) reported an average bacterial cell number of 5.4×10^8 cells/liter from the Antarctic, which is comparable with values from other seas (Williams, 1981).

Grazing by microzooplankton is a process of major significance. Ciliate protozoans, microflagellates, and pelagic rotifers can potentially remove a large fraction of daily plant production (see Caprulio and Carpenter, 1980, 1983). Linley et al. (1983) speculated that between 20 and 60% of primary production passes to the microbial/microzooplankton community. Williams (1981) suggested from model calculations that twice as much carbon reaches the next trophic level through microheterotrophs as that passing through larger herbivores. Despite the lack of information on Antarctic microbial/microzooplankton communities, recent studies indicate that ciliates and choanoflagellates will prove to be important grazers (Buck and Garrison, 1983; Hewes et al., in press).

Macrozooplankton

Knowledge of Antarctic macrozooplankton other than E. superba is so fragmentary that any discussion of their role in the food web can only be speculative. It is certain that, as in other oceans of the world, grazing by copepods is important. Indeed, in the Pacific Ocean sector copepods are probably the major macroplankton consumers of the phytoplankton bloom near the ice-edge. Salps are also very efficient grazers, and their fecal pellets are a major source of food for the benthos. Problems in estimating accurately the biomass of gelatinous zooplankton (salps, medusae, ctenophores, and siphonophores) continue to confound efforts to quantitatively describe this part of the food web.

The presumed slow growth rates of zooplankton in winter suggust that populations may be resource-limited seasonally. If summer populations are food-limited as well, the effects of exploiting a single component will be very different from the effect of harvesting a population with an unlimited food resource. Until more is known about interactions in the

Southern Ocean food web, predicting the effects of harvesting one or more components will be very difficult. When a better understanding of the annual primary production, the utilization of the primary production by the microzooplankton community, and the competitive interactions between the various macrozooplankton species is obtained we will be in a position to make informed judgments about the likely consequences of developing fisheries. At present, we cannot determine the manner in which perturbations such as krill harvesting will alter the interactions within the Southern Ocean food web. For this reason, Antarctic fisheries should only develop in small increments, accompanied by careful monitoring of selected indicator species as outlined in the companion document to this paper (Bengtson, 1984).

CHAPTER 3: ANTARCTIC KRILL

Introduction

Of the six common euphausiid species in the Southern Ocean (Euphausia crystallorophias, E. frigida, E. superba, E. tricantha, E. vallentini, and Thysanoessa macrura), E. superba, the Antarctic krill, is the most abundant and the focus of much scientific and commercial interest. The following review will primarily consider Antarctic krill, although some reference will be made to the other euphausiids (throughout this paper the term "krill" refers to E. superba). Further information on these species can be found in the following chapter as well as in John (1937), Nemoto and Nasu (1958), Baker (1959a), Marr (1962), and Baker (1965). Mauchline and Fisher's (1969) treatise on the biology of euphausiids has been recently updated by Mauchline (1980).

Despite the intensive research effort directed at E. superba, our knowledge of most aspects of the distribution and biology of krill is incomplete. As available information increases, however, improvements in sampling procedures and experimental techniques are occurring. These advances will allow further progress. Furthermore, the notion of the Southern Ocean as a relatively simple ecosystem dominated by a short food chain of primary production-krill-higher predators has been replaced by more complex trophic models. Changing ideas about interactions between the many components of the ecosystem are casting doubts on previously held assumptions as well as highlighting areas for future research.

Distribution

Geographic distribution

The distribution of krill was reviewed by Deacon and Baker (1980). Everson (1977) presented a detailed account of the distribution of eggs and early larvae, the vertical and horizontal distribution of the adults and also the various theories for the control of distribution. Generally, E. superba is distributed in a circumpolar band bounded to the north by the Antarctic Convergence. Krill have been reported north of the Convergence (Dall and Dunstan, 1957; Sasaki et al., 1968; Mackintosh, 1973) and also in a Chilean Fjord (Antezana et al., 1976) but these occurrences are probably aberrant. Major concentrations of krill occur in the East Wind Drift, Weddell Sea Drift, South Georgia area, Bellingshausen Sea, north of the Ross Sea, and near the Kergeulen Gaussberg Ridge (Marr, 1962; Nemoto, 1968; Mackintosh, 1973). The regular occurrence of such concentrations may indicate the existence of distinct populations or races (Makarov, 1974).

Although krill spawns throughout its range, Mackintosh (1973) cited 4 areas containing concentrations of the early larval stages: the East Wind Drift, Bransfield Strait area, and two divergence zones in the Scotia Sea and Weddell Drift. There are several theories to explain the

distribution of such concentrations. Marr (1962) suggested that krill maintain approximately the same position throughout their life. This result could be accomplished by swimming against prevailing surface currents or by vertically migrating between opposing currents. The latter seems unlikely as many krill observations indicate a maximum depth of approximately 250 m even though there are reports of krill at deeper depths (Shevtsov and Makarov, 1969). It is also possible that small-scale eddies around islands or submarine ridges could maintain krill in localized areas (Khvatskiy, 1972; Makarov, 1972).

Krill may also be carried by larger currents in a circulation pattern that maintains the concentrations. Examples of such patterns may be evident in the Weddell Sea, Ross Sea, and Kerguelen Gaussberg Ridge area (Marakrov, 1972). Makarov (1972) expanded on the early suggestions of Ruud (1932) for the Weddell Sea: he postulated that after spawning near the South Orkney Islands, larvae drift clockwise around the Weddell Sea twice before spawning in the South Orkneys. Fevolden (1979) indicated that it took 3 years for krill in the Weddell Sea to reach maturity. He also felt that size frequency analyses suggested that the Weddell Sea population was different from those further north. The distinction of a Weddell Sea population or sub-population was hypothesized by Maslennikov and Soliankin (1980) as well.

A very different area containing krill concentrations is that around the island of South Georgia. Marr (1962) felt that krill did not spawn successfully in this area and that the population originated elsewhere. Deacon (1937) reported Weddell Sea water flowing along the northeast side of South Georgia, indicating that the local population may have orginated in the Weddel Sea (Marr, 1962). However, the frontal zone between the Weddell Drift and the West Wind Drift is now thought to be well south of the island (Boganov et al., 1969). Hence, the krill population off South Georgia is now thought to originate from a source or sources other than the Weddell Sea. Everson (1976) concluded that the evidence for krill off South Georgia originating in the Bellingshausen Sea or Bransfield Strait was at best circumstantial, and Kock and Stein (1978) indicated that these krill did not originate in the Eastern Bellingshausen Sea. Therefore, the origin of krill from South Georgia remains difficult to ascertain.

Stock identification

Understanding the existence and degree of isolation of discrete populations within the circumpolar distribution is a key factor in understanding krill population dynamics. Identification of populations through protein (enzyme) electrophesis has been attempted with samples of krill by Fevolden and Ayala (1981) and Anderson (1982). Measurements of enzyme polymorphism from the Bellingshausen Sea revealed a relatively low level of genetic variation (Ayala et al., 1975). Fevolden and Ayala (1981), however, found a higher level of genetic variation in a krill sample from the Weddell Sea. These preliminary studies have formed the basis for work currently being undertaken. It seems likely that genetic

differences between geographic populations of krill may exist, although the degree of isolation of the various populations is unknown.

Abundance

Standing stock estimates by area

The only large-scale estimate of the abundance of E. superba by area was conducted by an international, multi-ship field effort entitled FIBEX (Hempel, 1983). A second phase of this program, SIBEX is currently underway. The following discussion is abstracted from a preliminary report of FIBEX estimates of krill abundance (Hampton, 1983). Table 6 presents estimates of the biomass and mean density of krill for each of the 5 FIBEX areas surveyed:

i) W. Atlantic Sector: ca. 65°W - 35°W, 55° - 65°S

ii) Indian Ocean Sector A: ca. 15°E - 60°E, ca. 60°S - 65°S

iii) Indian Ocean Sector B: ca. 60°E - 75°E, ca. 60°S - 65°S

iv) Pacific Sector A: ca. 120°E - 130°E, ca 60°S - 65°S

v) Pacific Sector B: ca. 160°E - 165°E, ca. 60° - 65°S

The total area surveyed encompassed approximately 2.1 million square km. In the West Atlantic Sector, highest densities occurred in the Bransfield Strait and near Elephant Island; lowest densities were present in the Southern Scotia Sea and the Drake Passage. High densities generally occurred around islands or over shelf areas whereas lower densities were found over deep water. One block of the Sector (near Elephant Island) covered an area of only 9% of the Sector but contained approximately 27% of the biomass observed. In the Indian Ocean Sector, highest densities occurred close to the continent with density and abundance generally increasing from west to east. In that Sector, 3 blocks, comprising only 8% of the total area surveyed, contained approximately 67% of the total estimated biomass. Both areas contained at least one very large swarm (superswarm). Hence, superswarms may contain a significant proportion of an area's krill biomass during the summer. The FIBEX survey also indicated a relatively high abundance of krill in the Indian Ocean Sector B, an area which has been little studied.

Total biomass

The estimation of krill biomass is complicated by the large geographic range of the species and a highly variable density of krill, resulting from its swarming behavior. Marr (1962) estimated a mean biomass of 2.5g/m^2 based on visual observations. He also recalculated data from Heyerdahl (1932) and increased this figure by an order of magnitude. If these estimates are assumed to be representative of the East Wind Drift and the Weddell Drift regions, they lead to an

Table 7. Estimates of the biomass and mean density of Euphausia superba for all sectors of FIBEX. These figures are point estimates within a particular season; abundance is known to vary between seasons. Data abstracted from Hampton (1983).

Sector	Area ($km^2.10^6$)	Biomass ± standard deviation (millions of tons)	Mean density ($g\ m^{-2}$)
W. Atlantic	1.03	11.33 ± 1.15	11.0
Indian A	1.89	11.77 ± 2.26	6.2
Indian B	0.89	54.12 ± 19.35	60.8
Pacific A	0.34	0.12 ± 0.05	0.4
Pacific B	0.41	0.25 ± 0.05	0.6
All sectors	4.56	77.59 ± 19.51	17.0

extrapolated estimate for total Antarctic biomass of 44.5 - 521 million tons (Everson, 1977). Makarov and Shevtsov (1972) estimated a total range of 953 - 1350 million tons, and Everson (1977) converted the estimate of Gulland (1970) to a wet weight of approximately 750 million tons. In making this estimate, krill were assumed to account for 50% of total zooplankton biomass. However, Voronina and Naumov (1968) and Voronina et al. (1979b) reported that euphausiids accounted for only about 10% of their catches. Further direct estimates of biomass are available from the FIBEX data summarized in Table 6 (Hampton, 1983). The estimate of total biomass for the area surveyed during FIBEX is 77.59 $\pm$ 19.51 million tons. Although this estimate is unsuitable for extrapolation to the entire Southern Ocean because sampling was non-random, a tentative figure of 200 to 600 million tons for the total biomass of E. superba has been suggested (Hampton, 1983).

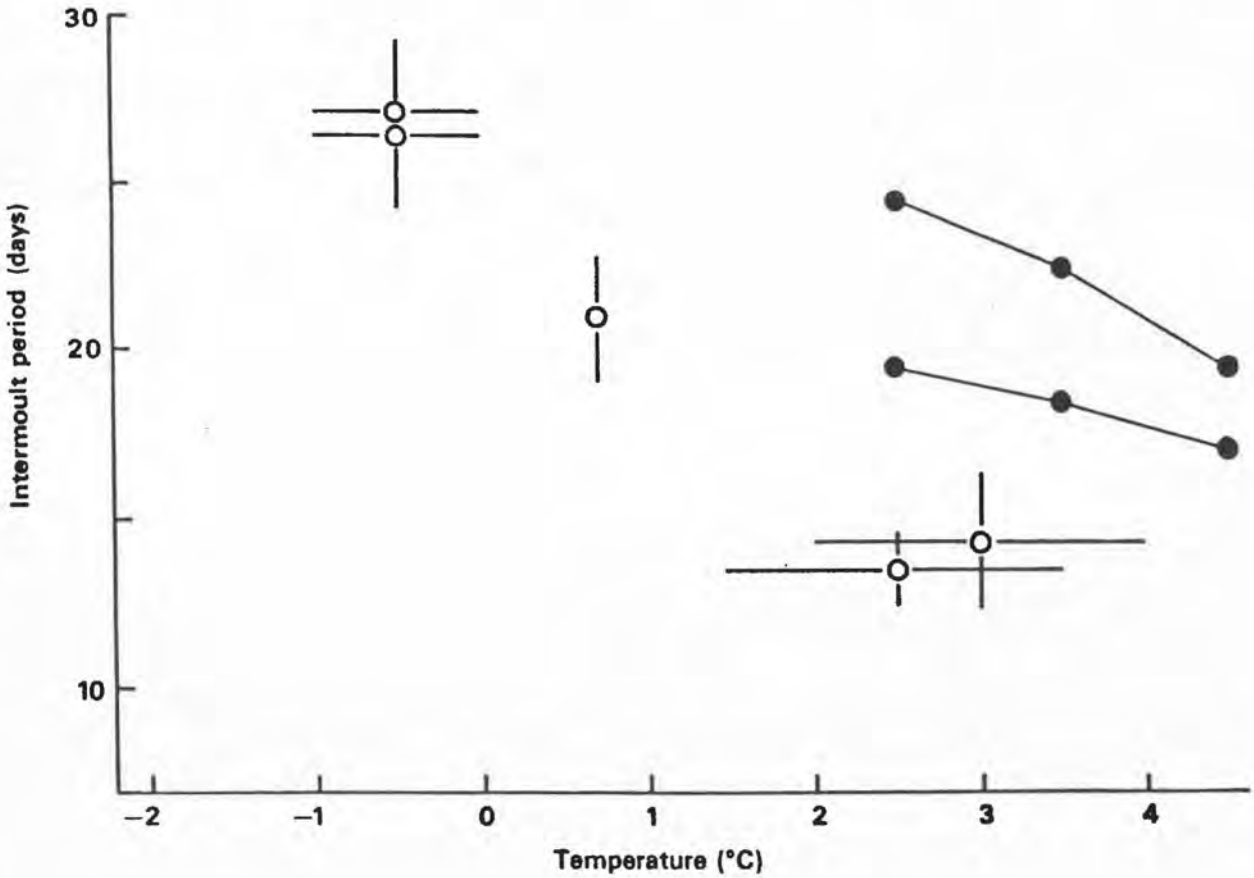
Everson (1977) summarized indirect estimates of krill biomass calculated from estimates of primary production and consumption by krill predators. Using a value of 50 g c/m^2 as an estimate of primary productivity, he calculated a wet weight for krill of approximately 10,000 million tons/year. Everson (1977, in press a) also has collated estimates of krill consumption by higher predators. Predators were estimated to consume less than 200 million tons of krill annually (see food habits sections in following chapters). Although these estimates suffer from insufficient information on predators' habits, squid and fish in particular, they are useful in providing another approach in approximating krill biomass.

Molting and Growth

The first studies of molting per se comprised the maintenance of low numbers of individuals in laboratory aquaria (Mackintosh, 1967; McWhinnie et al., 1976; Clarke, 1976). These authors reported very low growth rates which they considered unrepresentative of conditions in the field. Although recent studies have used improved techniques, low, zero, or even negative growth in the laboratory are still the norm rather than the exception (Murano et al., 1979; Buchholz, 1982; Ikeda and Dixon, 1982a; Poleck and Denys, 1982; Morris and Keck, in press). Together, these authors have provided data on the relationship between the intermolt period (IMP) and temperature (Clarke and Morris, 1983) (Fig. 2).

Numerous models for the growth of E. superba have been constructed using analyses of the size frequency distribution of samples (Ruud, 1932; Bargmann, 1945; Marr, 1962). These were summarized by Mackintosh (1972) and Everson (1977). Baker's (1959a) study of the growth of E. tricantha provides a useful comparison. All growth models for krill suffer from a lack of information on krill longevity and overwintering feeding strategy. The early models for growth curves indicated a 2-year life span, although the presence of an "intermediate group" of krill (Marr, 1962) complicated the interpretation. This group may represent an additional year class (Ivanov, 1970), an effect of early or late spawning (Mackintosh, 1972), the result of the mixing of krill from different

Fig. 2. Relationship between intermoult period and temperature for Euphausia superba. Reproduced from Clarke and Morris (1983). Open circles, data from Mackintosh (1967), Murano et al. (1979), Ikeda and Dixon (1982a), Morris and Keck (in press). Horizontal bars show the range of temperatures, vertical bars are standard deviations.



geographic areas (Makarov, 1971), or some effect of overwintering body shrinkage (Ikeda and Dixon, 1982a).

Analysis of body size suggested that the life span of E. superba ranges from 2 years (Rudd, 1932; Bargmann, 1945; Marr, 1962) to 3 years (Marr, 1962; Ivanov, 1970). These estimates have been cast into doubt by the observations of post-spawning reversion to immature forms (McWhinnie and Denys, 1978) and postulated shrinkage overwinter (Ikeda and Dixon, 1982a). Year-round morphometric data from krill at Admiralty Bay affirm an apparent seasonal body shrinkage (Stepnik, 1982) (Fig. 3). Etterschank (1983), using an analysis of the age pigment lipofuscin, detected the presence of 5 year classes in a krill population at Prydz Bay. If krill do indeed exhibit seasonal shrinkage, the use of body length for age determinations might lead to underestimates of krill ages. Further evidence of a greater longevity than previously estimated comes from the maintenance of a nominally 2 year old krill specimen for a period of 5 years in the laboratory (Ikeda, unpublished data). The extent to which krill survive to 5 years and more in the field is as yet unknown, but further studies using the measurement of lipofuscin promise greater insights into the age structure of krill populations in various locations.

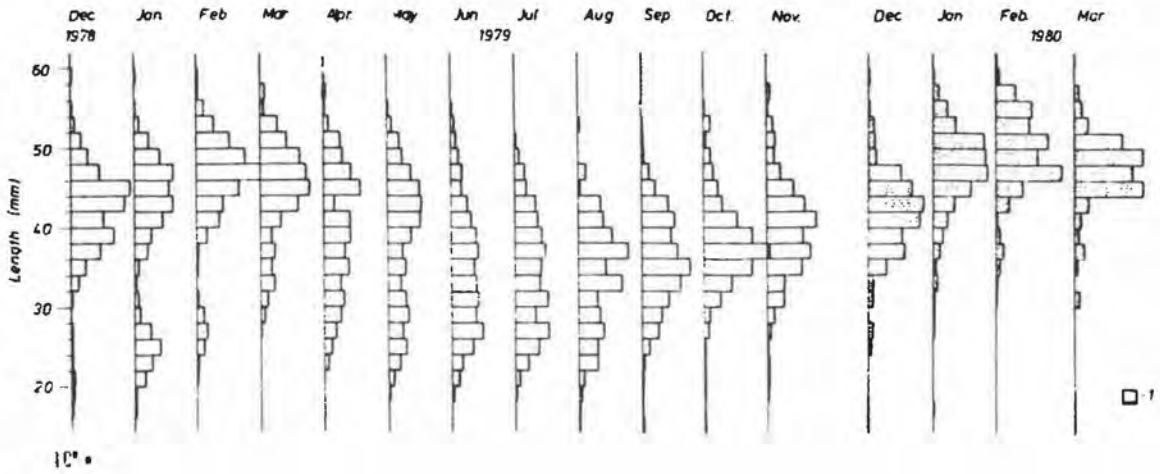
Until the questions of longevity and overwintering strategy are resolved, a convenient framework within which to work are the hypothetical curves of Mauchline (1980) which provide for growing seasons of 120, 150, and 180 days. The latter model was used by Clarke and Morris (1983) in their preliminary summmer energy budget for krill off South Georgia. These authors also report that the increase in median length of samples taken from a patch off South Georgia in the summer over 6 consecutive days was of the order of that predicted by Mauchline (1980). This 6-day study also resulted in models of both feeding (Morris and Ricketts, 1984; Morris et al., in press) and molting (Morris, in prep). Such studies indicate the feasibility and value of research monitoring a patch of krill over relatively long periods.

Behavior

The characteristic formation of dense aggregations by Antarctic krill is well known. Several terms have been applied to these groups, including schools, swarms, shoals, and superswarms (Mauchline and Fisher, 1969; Mauchline, 1980). The phenomenon itself is of great importance, for aggregating is a key feature of the krill's ecology and affects krill's commercial exploitation, consumption by predators, and estimation of abundance.

The underlying mechanisms governing the formation, persistence, and dispersal of aggregations are not clear. There is evidence that feeding and molting behavior are linked to aggregations (discussed later). Marr (1962) and Naumov (1962) suggested that some aggregations may be spawning concentrations. Shust (1969), Nakamura (1973), Iarogov (1979), and Kubota (1981) indicated that light intensity may be involved in aggregating behavior. But observations of krill aggregations at the

Fig. 3. Annual changes in the body size distribution of Antarctic krill (Euphausia superba) collected monthly in Admiralty Bay, King George Island, South Shetland Islands. (From Stepnik, 1982).



surface during the day (Ozawa et al., 1968) appear to conflict with that idea. Ruud (1932), Beklemisher (1961), and Boganov (1974) suggested that turbulence and eddy currents may form swarms. Everson (1977) considered the effects of such small-scale currents more applicable to areas of "high average abundance" such as superswarms.

Aggregation size and density

The sizes and shapes of krill aggregations range from swarms a few to a few hundred meters across the maximum dimension (Marr, 1962; Witek et al., 1981; Hamner, in press) to patches covering several hundreds of square km containing a high abundance of krill in swarms (Mauchline, 1980; Everson, 1982). Considerably smaller areas of very high abundance have been termed superswarms. Macaulay (1981) estimated that a superswarm off Elephant Island in 1981 contained a biomass of some million tons of krill.

Estimates of krill density in aggregations vary considerably, as a function of both the type of aggregation and the methodology used in the estimation. Estimates using acoustic detection in conjunction with net hauls range from 10 - 16 kg/m^3 (Moiseev, 1970), "up to 15 kg/m^3" (Makarov et al., 1970), to 33 kg/m^3 (Nemoto and Nasu, 1975). Mathisen and Macaulay (1983) reported peak values of 16 kg/m^2 for a superswarm off Elephant Island. If krill were evenly distributed throughout the top 100 m, that figure would represent an average density of approximately 160 g/m^3. Everson (1982), working on a patch off South Georgia, reported densities of approximately 10 individuals/m^3 at night (krill dispersed throughout the water column) and approximately 145 individuals/m^3 by day (krill concentrated in swarms). When extrapolated with echosounding data, these values yield estimates for density in swarms of approximately 0.1 - 30 km/m^3. Hamner et al. (1983) reported diver visual estimates of 20,000 - 30,000 m^3 per school of krill. Although the shape of schools varied, typical dimensions were 100 m long, 3 - 4 m wide, and 10 m deep. If, as suggested by Marr (1962), the majority of krill biomass is contained in aggregations, then understanding the structure, function, and density of these groups will be of great importance in further studies of krill ecology.

Swarming, feeding, and molting

One of the major functions attributed to the formation of krill aggregations is that of feeding. Shust (1969) suggested that swarming was a transient phenomenon specifically related to feeding. Pavlov (1969) proposed a model relating feeding, vertical migration, swarming, and dispersion in a regular cycle. He suggested that feeding and swarming were mutually exclusive events. Morris et al. (1983) presented laboratory evidence of a marked decrease in filtration rate as krill density rose. In contrast, Antezana and Ray (in press) suggested feeding and swarming occur simultaneously. These authors felt that superswarms have an adaptive value for locating and exploiting ephemeral, patchy food resources. Morris et al. (in press b) found no effect of the presence of

swarms on the levels of chlorophyll found in the alimentary tracts of krill. These authors, however, expressed reservations about the interpretation of chlorophyll levels in krill caught in nets because chlorophyll turnover rates in the gut are on the order of minutes (Morris, in press).

Feeding studies off South Georgia have indicated the importance of molting behavior in relation to both feeding and swarming (Morris and Ricketts, 1984; Morris et al., in press). Feeding and molting are mutually exclusive events, but there is some evidence for synchronous molting within swarms, implying a prolonged group homogeneity. Morris (in prep.) modelled the relationship among environment, feeding, molting, and swarming for krill off South Georgia. This model reproduced in a simplified form in Figure 4. The occurrence of krill in swarms does not imply the absence of krill in the dispersed state. A small vertical migration in swarms at night, accompanied by an increase in the mean horizontal chord of the swarms, is paralleled by a rise to the surface layer. Molting occurs both in the afternoon and during the night. Morris' model is presented as an example of the hypothetical interactions among molting, swarming, and feeding rather than a system applicable to krill in all areas.

Daily and Seasonal Movements

Closely linked to the mechanisms affecting the formation of aggregations is the vertical migration of krill (Everson and Ward, 1980). The vertical migration of E. superba is not from deep water in the day to the surface waters at night as found with E. tricantha or E. frigida (Mauchline and Fisher, 1969). The observed patterns of vertical migration in E. superba are varied but occur primarily in the top 100 m (Fig. 5). Observed migration patterns include diurnal changes in the depth of swarms, dispersion and aggregation, and migration to the surface at night (Pavlov, 1969; Fischer and Mohr, 1978; Everson, 1982, in press a).

Horizontal movements of krill have been reported at speeds of some 6 - 30 cm/s (Kils, 1979; Hamner, in press), with higher speeds occurring during escape reactions (Hamner et al., 1983). The observed variation in swimming speeds related to size have been postulated as a possible sorting mechanism for swarms (Kils, 1981; Hamner et al., 1983). On a broader scale, Kanda et al. (1982) tracked 2 swarms of krill swimming for 74.5 km and 186.6 km at average speeds of 0.42 - 0.47 km/h and local speeds of 1.21 km/h. The authors consider these to be examples of spawning migrations. This sustained horizontal movement was probably against northwesterly current (indicated by iceberg movement) of 0.29 km/h.

An oversimplified extrapolation provides some indication of the potential scope of krill horizontal migration. Ignoring any reduced or increased speed over the ground due to currents, a sustained migration at approximately 0.48 km/h would be equivalent to more than 4,000 km per

Fig. 4. A model of the relationship between feeding, swarming, vertical migration and moulting for Euphausia superba off South Georgia.

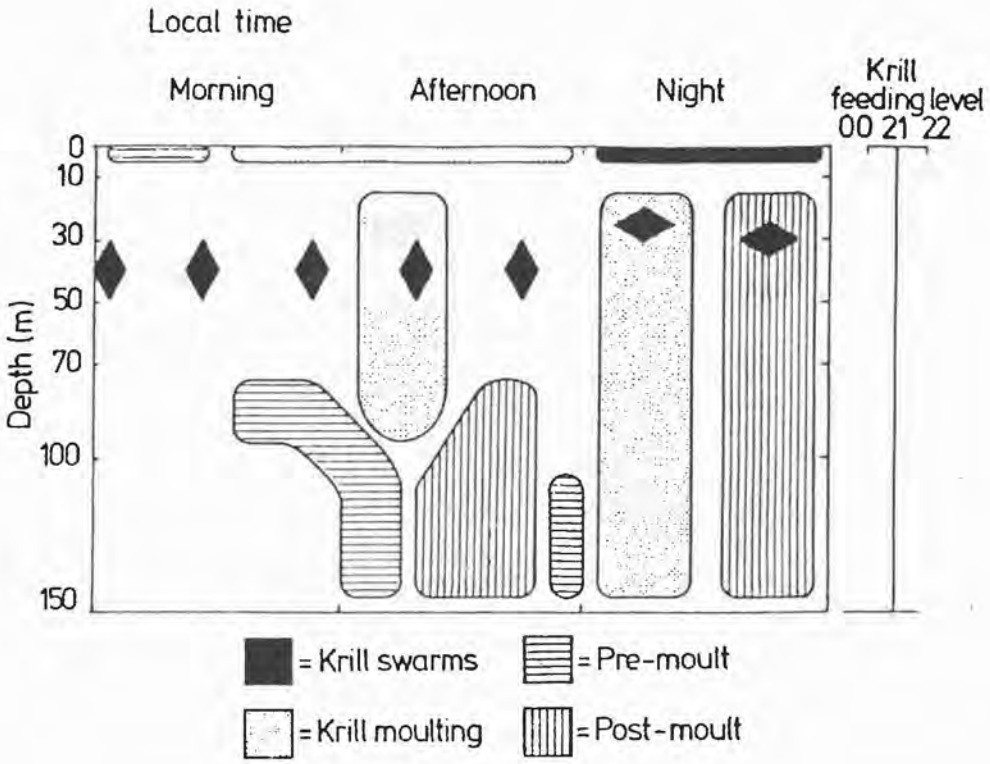
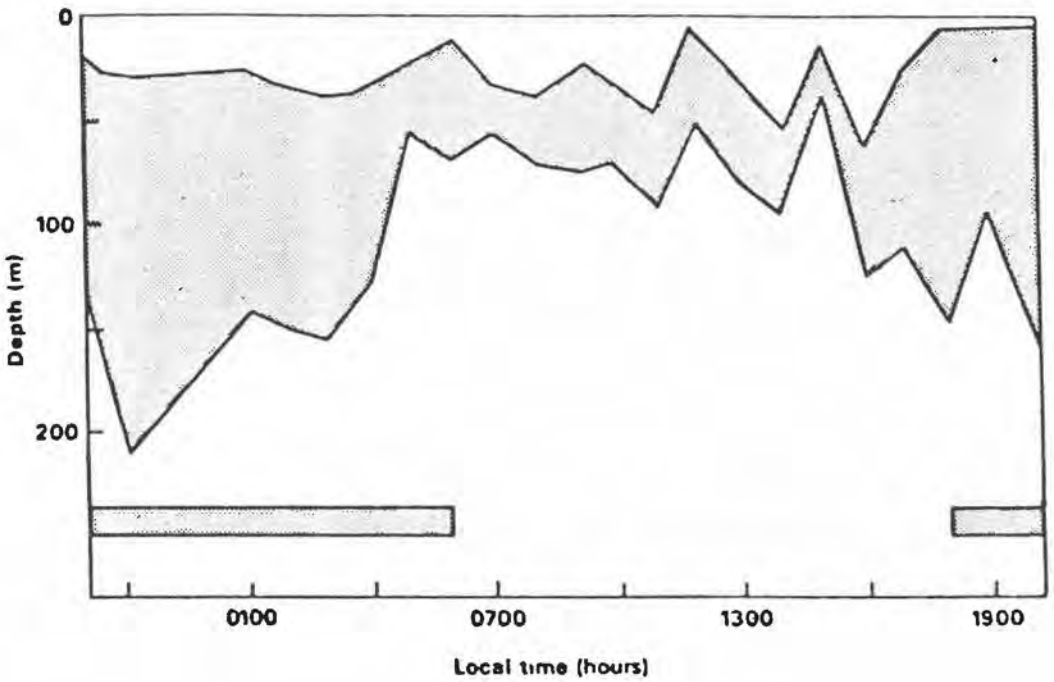


Fig. 5. Euphausia superba. Diurnal variation in krill dispersion within the water column for a patch of krill over the South Georgia continental shelf (depth < 350 m). The upper level is the mean depth of the top of swarms, within a 2-h time block, the lower level is the mean depth of the bottom of the swarms (redrawn, with permission, from Everson, 1982). Bar marks the period of darkness. (From Morris, Ward, and A. Clarke, 1983).



year. Such possibilities emphasize the need to understand the aggregations and movements of E. superba both as a localized phenomenon and as a potential factor in its distribution.

Reproduction

Comprehensive descriptions of the reproductive biology of E. superba were given by Fraser (1936) and Bargmann (1937), with a generalized summary for euphausiids in Mauchline and Fisher (1969). Gravid and spent females are reported between November and April indicating a peak of spawning activity in February and March (Mackintosh, 1972). The timing of peak spawning is affected by latitude (northerly areas peak earlier) and by annual temperature variation (Makarov, 1973). During warm years the early disappearance of sea-ice leads to an early phytoplankton bloom, an early start to the growing season, and an earlier krill spawning period. Makarov (1975, 1976) also reports a difference in the timing of spawning between first- (late season) and second- (early season) time spawners.

There is a wide range of estimates for the fecundity of E. superba, dependent upon the techniques used for estimation (Mauchline and Fisher, 1969; Makarov, 1975). These are summarized by Everson (1977) who explained that some of the highest estimates, for example, Bargmann's (1937) estimate of 11,000 eggs, may be an indication of all the eggs in the ovary, at various stages of development, rather that an indication of the number of eggs released at a given time. This problem occurs in a number of estimates of fecundity, as does confusion over the size of the eggs counted. Naumov (1962) quoted a maximum egg number of 3,590 which Everson calculated to be equivalent to approximately 60% of the body volume if all eggs counted were the size given by Naumov. Everson (1977) pointed out that some eggs counted were released in a second spawning season; this pattern emphasizes the need to distinguish between estimates of seasonal and total fecundity. Kikuno (1981) timed spawning as occurring in approximately 50 minutes, and estimated 1,140 - 1,688 eggs released per female. Denys and McWhinnie (1982) measured 2,200 - 8,800 eggs released per female in biphasic spawning in the laboratory. The spawning periods occurred 14 days apart, with post-spawning regression to juvenile maturity stages over a period of some six weeks. Recent work by Ross and Quetin (1983) suggests multiple spawning (9 - 19 times) in a season, with an interval of approximately 7 days. These authors estimated that approximately 2,500 eggs were released per female per spawning event. Jazdzewski et al. (1978) estimated a fecundity of 2,300 - 13,500 eggs. Clarke (1980), using a biochemical estimate of fecundity, indicated the production of some 7,000 - 15,000 eggs. It seems likely, therefore, that perhaps 1,000 - 2,000 eggs are released per spawning, and that repeat spawnings during a season will raise the total number of eggs produced to the upper ranges of egg production estimated by various authors. These seasonal high estimates of fecundity must be combined with data on the longevity of krill to estimate life time fecundities.

Several other aspects of krill reproduction are being investigated. A simple classification of the stages of sexual maturity has been devised (Makarov and Denys, 1981) allowing the comparison of both samples and populations. McWhinnie et al. (1979) were able to maintain krill in the laboratory over winter and observe changes in body size, mating, and spawning. George (1980) has suggested that pressure is of importance in the development of the early stages of krill; however, Kikuno (1981) observed egg development at atmospheric pressure. He reported a hatching period of 7 days (followed by an 118 day development to meta-nauplius stage), which agrees closely with a calculated hatching period of 8 - 9 days (Mackintosh, 1972). The energetic costs of reproduction in krill are little known, but current estimates have been incorporated into a recent energy budget (Clarke and Morris, 1983).

Fraser (1936) described the life histories of young stages and Bargmann (1945) those of the adolescents and adults. Mackintosh (1972) suggested that the life cycle is related to ice and water conditions. An overall description of the natural history and geography of the species is given by Marr (1962).

Eggs (approx. 0.7 mm diameter) are spawned at the surface between November and April, with a peak in February-March (Everson, 1984a); eggs sink, undergo cleavage, and hatch at depths up to approximately 1800 m. The hatched nauplii rise, develop through a metanauplius stage, and reach a calyptopis stage at the water surface. There are three calyptopis stages (length approx. 1 - 5 mm), followed by 5 furcilial stages (5 - 11 mm); post-larval adolescent krill (12 - 35 mm) and adults (35 - 60 mm) occupy approximately the top 100 m during a 2-year development to reproductive maturity.

The timing of the above stages and the depth ranges occupied by each apparently varies between areas. Siegel (1982) reported a delay in the timing of spawning in the East Wind Drift area of the Southern Weddell Sea compared to the Antarctic Peninsula/Scotia Sea region. In addition, he indicated that it takes 3 years for krill to reach sexual maturity in this region (as suggested by Fevolden, 1979), compared to two years in more northerly populations. The maximum depth recorded for eggs (approx. 1800 m) may either be the result of the physical limitations on sinking eggs (such as the boundary of the Antarctic Bottom Water) (Voronina, 1974) or it may represent the maximum depth from which larvae can successfully migrate to the surface water without exhausting their limited food reserves. Early suggestions that spawning occurs on the bottom in the shelf zone (Fraser, 1936) or that spawning occurs primarily in the shelf zone (the early larvae being transported from the shelf to oceanic waters in the Cold Bottom Water) (Marr, 1962) have been superceded. It is now thought that spawning occurs primarily in oceanic waters, probably throughout krill's geographic range (Voronina, 1974).

Following the period of larval developmental ascent (a phenomenon also characteristic of other Southern Ocean euphausiids such as E. frigida, E. tricantha, and Thysanoessa (Makarov, 1978)), adolescent and

adult Antarctic krill occupy the surface layer above the Warm Deep Water (Marr, 1962). There are, however, some records of krill below this top 100 m layer (Pavlov, 1969; Shevtsov and Makarov, 1969; Permiten, 1970; Fischer, 1976; Nast, 1979). In contrast, E. frigida and E. tricantha have vertical migration patterns which daily take them from the Warm Deep Water to the surface waters at night.

Food Habits

Many types of food have been found in the stomach contents of krill, ranging in size from phytoplankton, such as diatoms or dinoflagellates; microzooplankters, such as tintinnids and radiolarians; to larger zooplankton species, usually found as fragments (Barkley, 1940; Hart, 1934: Hustedt, 1958; Marr, 1962; Nemoto, 1968). Krill are also reported as feeding on detritus (Pavlov, 1971), algae on the underside of sea ice (Hamner, in press), and other krill in laboratory settings (McWhinnie and Marciniak, 1964). Whereas krill is often considered an herbivore in a simplistic phytoplankton-krill-predator food chain, it is probably more accurate to think of krill as an omnivorous species which consumes phytoplankton heavily during the spring bloom.

Seasonal aspects of the feeding ecology of krill are characterized by sharp fluctuations in primary production and phytoplankton abundance between summer and winter. In early summer the phytoplankton bloom is dominated by larger species of algae, whereas smaller species are prevalent in both biomass and primary production during the rest of the summer. The versatile feeding mechanisms of krill (Kils, 1983) probably allow the exploitation of both types of phytoplankton. During winter, when both phytoplankton biomass and primary production are low, an alternative feeding strategy is required. Krill apparently can switch from detritus-feeding omnivory or carnivory to utilizing their own body protein (leading to body shrinkage).

The degree of herbivory in the summer is less clear, but likely is high. In the winter, when both primary production and the standing crop of phytoplankton are low, krill employ a different feeding strategy. Unlike the strictly herbivorous E. crystallorophias, which synthesizes an overwintering store of wax ester during the summer (Littlepage, 1964), E. superba stores lipid as triacylglycerol rather than wax ester (A. Clarke, 1980, in press a) and there is only equivocal evidence for the synthesis of an overwintering lipid store. The absence of such a store means that krill must survive either by feeding omnivorously (including ice algae) or, as suggested by Ikeda and Dixon (1982a) by metabolizing body protein. Field data on the overwintering strategy of krill are scarce, but krill with chlorophyll in the alimentary tract have been observed in late winter (Morris, unpublished data). Other krill, observed earlier in winter had empty alimentary tracts. Perhaps krill metabolize body tissue in the absence of food, and utilize food resources from sea-ice algae to detritus when they become available.

A greater appreciation of the potential feeding strategies of krill can be obtained from an examination of their feeding apparatus. Proposed feeding mechanisms of krill can be grouped into two models: a mechanical sieve model (Kils, 1982; McClatchie and Boyd, 1983) or a model surface chemistry and particle electrical charge model (Clarke and Morris, 1983). The mechanical model explains the selectivity of particles size observed in krill (Meyer and El-Sayed, 1983; Morris, in press). In the other model, the major water flow is over rather than through the mesh, thereby reducing the theoretical energy costs of pumping large amounts of water through a fine mesh mechanical sieve.

Estimates of the filtration rates of krill vary from tens of milliliters per hour to tens of liters per hour, depending upon the experimental technique employed (Morris, in press). It is likely that the actual amounts of water filtered are of the order of liters per hour, but until the mechanisms of filter feeding and the degreee of omnivory are understood, our knowledge of the energetic costs of feeding activity will remain limited. The importance of such an understanding is illustrated by the possibility of krill filtering nanoplankton (less than 20 um diameter) as postulated by Kils (1982), McClatchie and Boyd (1983), and Clarke and Morris (1983) and later observed by Morris (in press). Access to nanoplankton as a food resource could be of great importance in the overall feeding strategy of E. superba. In 24 stations in the Bellingshausen Sea and off South Georgia, nanoplankton comprised approximately 70% of the phytoplankton biomass (Von Brockel, 1981). Nanoplankton was also responsible for some 90% of the primary production, highlighting the importance of this group compared to the large species of diatoms and dinoflagellates (100 - 300 um) which predominate during the spring bloom (Hart, 1934; Uribe, 1982).

CHAPTER 4: ANTARCTIC CEPHALOPODS

Introduction

The role of cephalopods in the Antarctic marine community remains a partial enigma. Pelagic squid represent potentially one of the most important components of the Antarctic marine food web. They are both major predators of Antarctic krill as well as important prey for a variety of vertabrate predators. Squid are fast-swimming, active predators with well developed nervous systems (Brandt, 1983). They are difficult to catch, and for this reason research efforts have been hampered. It is clear that development of effective research techniques is needed to further investigate the role of cephalopods in Antarctic waters (for a useful review of techniques, see Hedgepeth, 1983).

Species Composition

Approximately 72 cephalopod species are known or thought to occur south of the Antarctic Convergence (Table 8). Of these, 55% are considered endemic to that area (Filipova, 1972). Due to the difficulty of catching cephalopods in nets and other sampling gear, many species are known only from the stomach contents of predators. For example, M. Clarke (1980) made a detailed study of Antarctic cephalopod species collected from sperm whale stomach contents (Figs. 6 and 7). There are almost certainly a number of Antarctic species in existence which are new to science and for which no description is yet available (Roper, 1969, 1981; SCAR/SCOR, 1983a).

Distribution

Most species of Antarctic squid are thought to be circumpolar, although certain species appear to occur in restricted localities (Everson, 1977). For example, some species off the coast of Durban, South Africa, may be restricted to the continental slopes, whereas others are not (Fig. 8). The distribution of Bathyteuthis abyssicola is circumpolar, although populations are more prevalent in some areas (Roper, 1969). This species is most often caught in circumpolar water of relatively high salinity and temperatures 1.25° - 2°C and in circumpolar-transitional water at lower salinity and higher temperatures (34.65‰ and 2° - 2.35°C, respectively) (Roper, 1969). High latitude waters support predominantly pelagic squids whereas octopods are more common nearer the sub-Antarctic islands (Roper, 1981).

There is some indication that Antarctic cephalopods may undertake seasonal migrations similar to those exhibited by northern cephalopods (Squires, 1957). M. Clarke (1983) provided evidence that Todarodes, Faningia, and Moroteuthis may make long seasonal movements following the advance and retreat of the ice edge. The seasonal change in the abundance of various species found in sperm whale stomachs off of South Africa and South Australia (Fig. 9) may be due to squid and/or whale migrations.

Table 8. Cephalopod species in Antarctic waters as determined by capture in scientific sampling gear and presence in predators' stomachs. Data from Roper (1969, 1981), Fillipova (1972), Everson (1977), and M. Clarke (1980). (After Bengtson, 1984).

Architeuthidae
- Architeuthis sp

Thysanothetuthidae
- Thysanoteuthis rhombus

Ommastrephidae
- Todarodes sp.
- T. filippovae
- T. argentinus
- T. sagittatus
- Nototodarus sloani
- N. gouldi
- Ilex argentinus
- Martialia hyadesi
- Symplectoteuthis oualaniensis
- S. luminosa
- Dosidicus gigas
- Ommastrephes pteropus
- O. bartrami

Onychoteuthidae
- Onychoteuthis banksii
- Kondakovia longimana
- Moroteuthis robsoni
- M. ingens
- M. knipovitchi

Gonatidae
- Gonatus antarcticus

Octopoteuthidae
- Octopoteuthis rugosa
- Taningia danae

Mastigoteuthidae
- Mastigoteuthis sp.
- Mastigoteuthis A.

Histioteuthidae
- Histioteuthis sp.
- H. bonelli
- H. atlantica
- H. eltaninae
- H. macrohista
- H. miranda
- H. meleagroteuthis

Psychroteuthidae
- Psychroteuthis sp.
- Psychroteuthis glacialis

Neoteuthidae
- Alluroteuthis antarcticus

Brachioteuthidae
- Brachioteuthis riisei
- B. picta

Bathyteuthidae
- Bathyteuthis abyssicola
- Batoteuthis scolops
- Neoteuthis sp.
- Promachoteuthis sp.
- Oregoniateuthis lorigera
- Calliteuthis miranda
- Crystalloteuthis glacialis
- Teuthowenia antarctica
- Taonius pavo

Cranchiidae
- Galiteuthis aspera
- G. glacialis
- Mesonychoteuthis hamiltoni

Loliginidae
- Loligo sp.
- L. braziliensis
- L. patagonica

Octopodinae
- Alloposus sp.
- Megaeledone senoi
- Thaumeledone brevis
- Octopus sp.
- Benthoctopus levis
- B. eureka
- B. berryi
- B. thielei
- B. magellanicus
- Pareledone sp.
- P. charcoti
- P. turqueti
- P. polymorpha
- P. harrissoni
- P. adelieana
- P. nigra
- P. antarctica
- Eledone massyae

Bathypolypodinae
- Graneledone antarctica
- G. microtyla

Fig. 6. Areas and positions where collections of sperm whale stomach contents were made. (From M. Clarke, 1980).

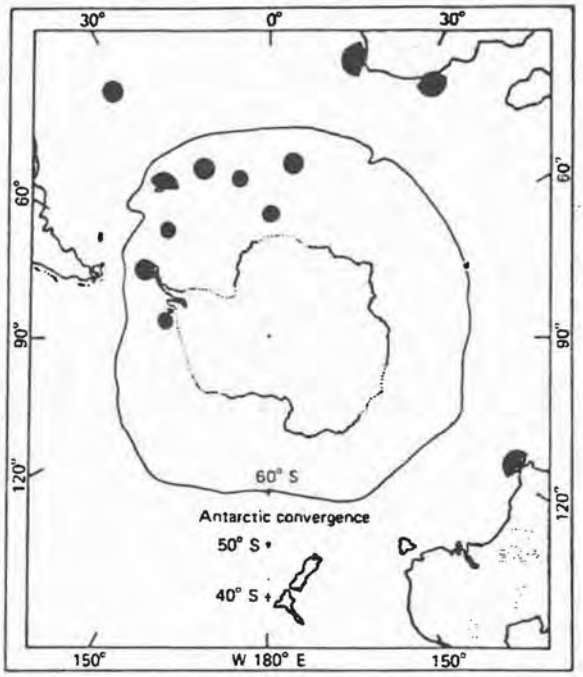


Fig. 7. Cumulative percentage curves comparing the species composition of beaks collected from stomachs of whales killed in the Antarctic. Sample sizes are shown. (From M. Clarke, 1980).

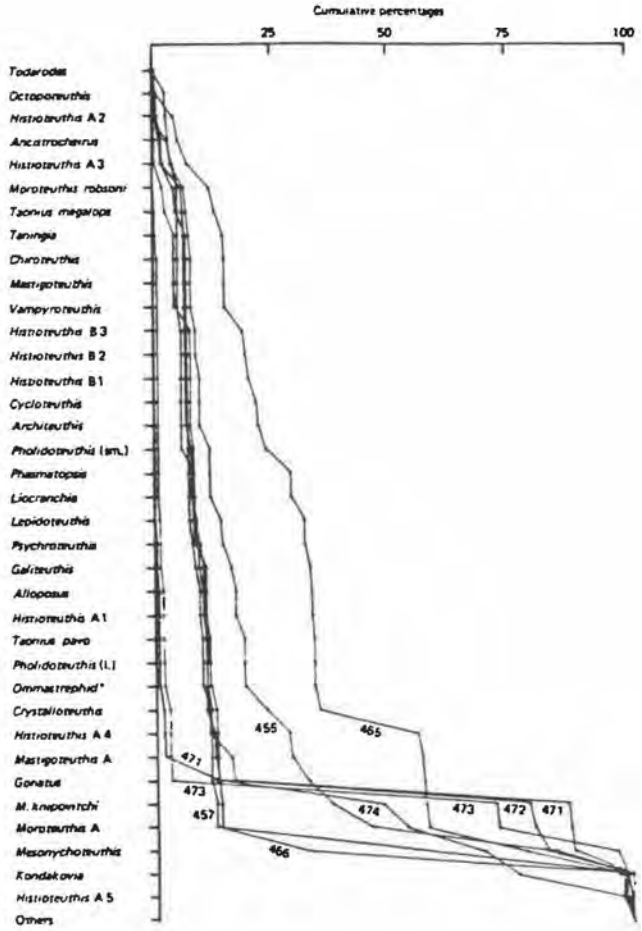


Fig. 8. Vertical distribution of selected cephalopods eaten by sperm whales superimposed on the bottom contour along the 150° line off the Durban beacon. Midwater depth ranges are based upon general knowledge of the vertical distribution of each genus or species. Depths at which species have been collected on the bottom either from trawls or from the stomachs of bottom fish are shown as stars. Depths of spawning are derived from the position over the slope at which spawning squid were recovered from stomachs of whales which were killed. See text for fuller explanation. (From M. Clarke, 1980).

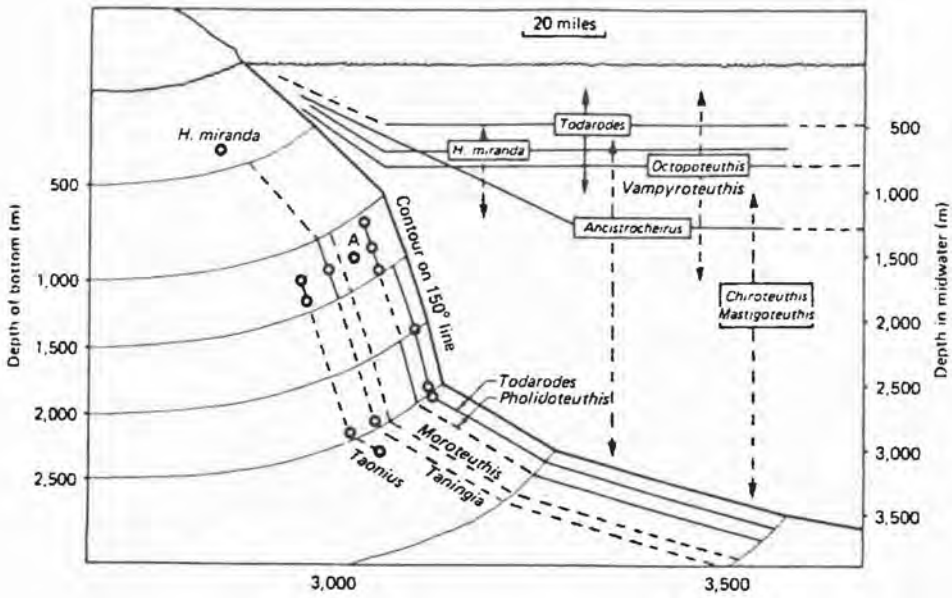
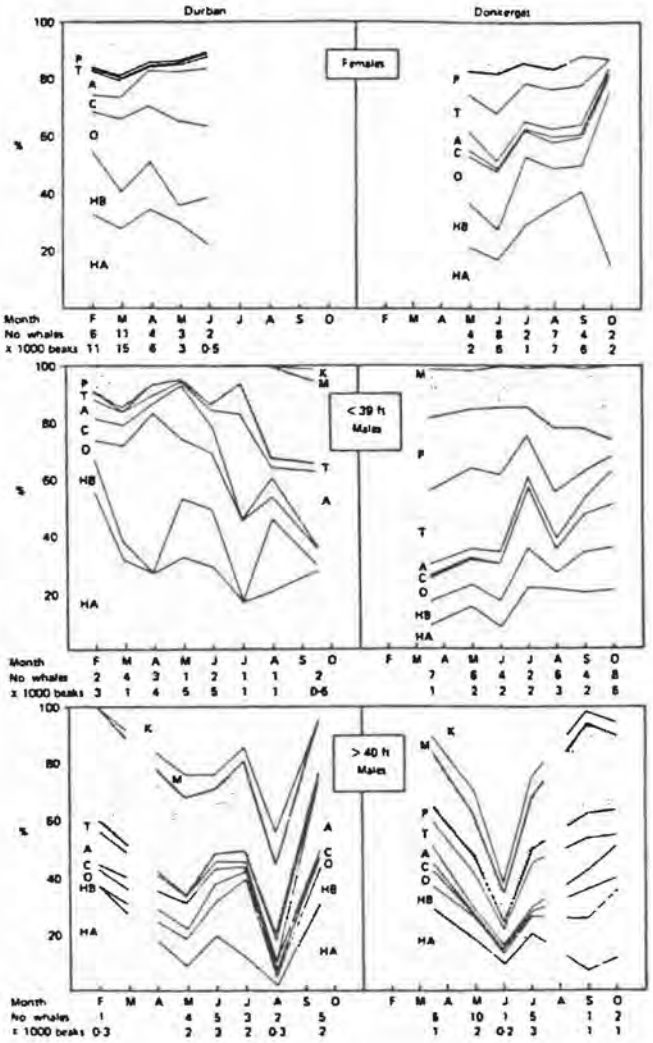


Fig. 9. Seasonal changes in the percentage species composition of beaks from female whales (top), male whales less than 39 ft long (center), and male whales more than 40 ft long (bottom) at Durban (left) and Donkergat (right). The number of whales sampled and the number of beaks (to the nearest thousand) collected are given. The main Antarctic species are included at the top of each graph and are separated from the main local species by the 'other', or less numerous species (stippled). HA = Histioteuthis A; HB = Histioteuthis B; O = Octopoteuthis; C = Chiroteuthis; A = Ancistrocheirus; T = Taonius megalops; P = Pholidoteuthis; M = Mesonychoteuthis; K = Kondakovia. (From M. Clarke, 1980).



The vertical distribution of cephalopods varies between species (Roper, 1969; Roper and Young, 1975; Zuev and Tzimbal, 1982). Figure 10 compares this distribution for selected Antarctic species. M. Clarke (1980) also noted that some species of squid descend in the water column as they mature. Within a range of preferred depths, a daily vertical migration is thought to occur and is correlated with night/day cycles (M. Clarke, 1977).

Abundance

Because different sampling methods catch cephalopods of different sizes and at different rates (Figs. 11 and 12), estimates of abundance calculated from these data will be biased (M. Clarke, 1977; SCAR/SCOR, 1983a). At the present time, however, obtaining data from scientific sampling gear, from predators' stomachs, and as by-catch of fisheries are the only methods available.

The most abundant cephalopods, as estimated from beaks present in sperm whale stomachs in the Antarctic, are Onychoteuthids and Cranchiids, representing 53% and 23% respectively (M. Clarke, 1983). Using a known relationship between body size and beak size of squid, it is possible to estimate the biomass of squid eaten by predators (Clarke, 1962). The annual consumption of squid worldwide is estimated to be well over 100 million tons (M. Clarke, 1983). Over 36 million tons of this amount is estimated to be taken by mammals and birds in the Antarctic (Table 9).

Reproduction and Growth

Very little is known about reproductive activity and growth in Antarctic cephalopods. McSweeney (1978) described the reproductive organs of Galiteuthis glacialis and the physical charateristics of a gravid female of the same species. He speculated that when spawning, eggs are released in a gelatinous mass rather than freely shed. Data on growth rates and longevity for Antarctic cephalopods are very sparse. McSweeney (1978) speculated that in Galiteuthis glacialis, large numbers of eggs are produced, followed by rapid growth, spawning, deterioration, and death. Voss (1973) felt that many squids are short-lived, maturing at one year of age and dying after a single spawning. However, recent work evaluating the growth rings in squid statoliths (Spratt, 1978; Kristensen, 1980) suggests that these structures can be used to determine the age of individuals, which may be several years old.

Food Habits

Although it is known that several species of Antarctic squid feed on krill (Marr, 1962; Dell, 1965; Nemoto et al., 1984) food habits are poorly known. Filipova (1972) suggested that many squid species were specialist predators on Antarctic krill. He noted that some species, such as Kondakovia longimana, have not been found outside areas where krill are present. Everson (1981) estimated that the annual consumption of krill by cephalopods may be as much as 100 million tons. When

Fig. 10. Vertical distribution of (A) Antarctic Bathyteuthis abyssicola captured by standardized 2-hour tows, (B) Crystalloteuthis glacialis Chun, 1906. Antarctic, (C) Brachioteuthis picta Chun, 1910. Antarctic, and (D) Gonatus antarcticus Lönnberg, 1879. Antarctic. (From Roper, 1969).

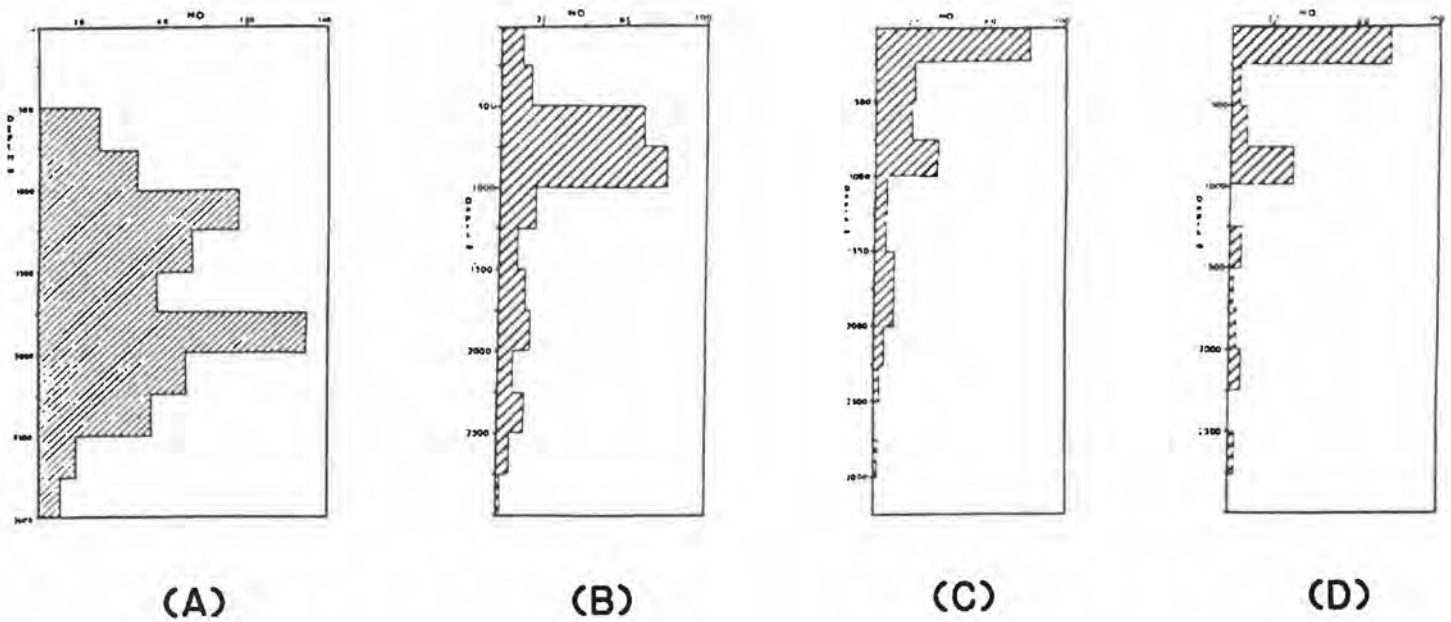


Fig. 11. Cumulative percentage curves for samples of beaks from Weddell seals and sperm whales in the Antarctic, and for squids caught by IKMT nets on a cruise of Eltanin (Roper, 1969). Stars indicate two families which occur at South Georgia in whale stomachs but are probably near the southernmost limit of their distribution. (From M. Clarke, 1977).

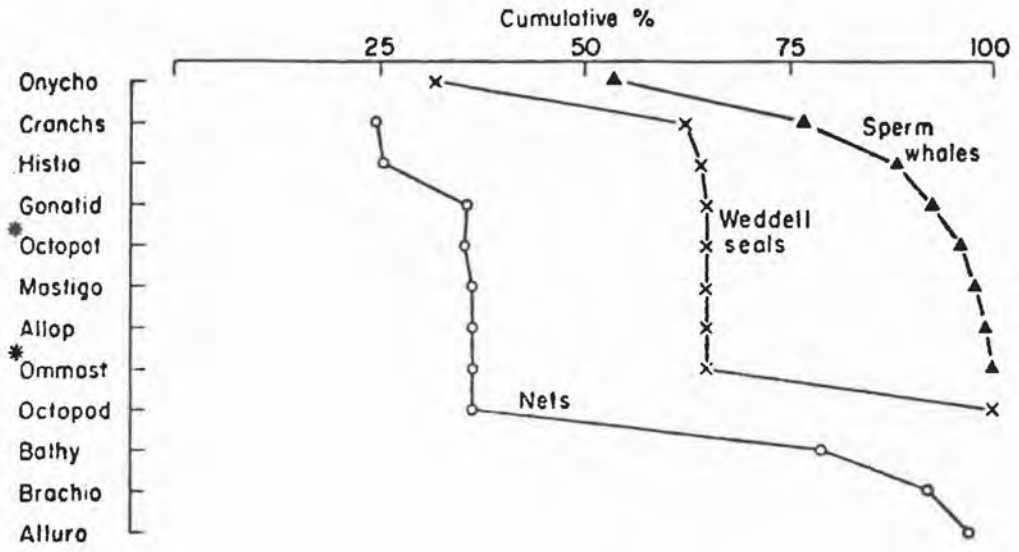


Fig. 12. The families of oceanic cephalopods (mainly squid) found in sperm whale stomachs and caught in research nets ($9m^2$ mouth opening) and commercial trawls in three areas of the North Atlantic. The whales eat histioteuthids, cranchiids, and octopoteuthids primarily. Nets catch squids mostly from other families. (From M. Clarke, 1983).

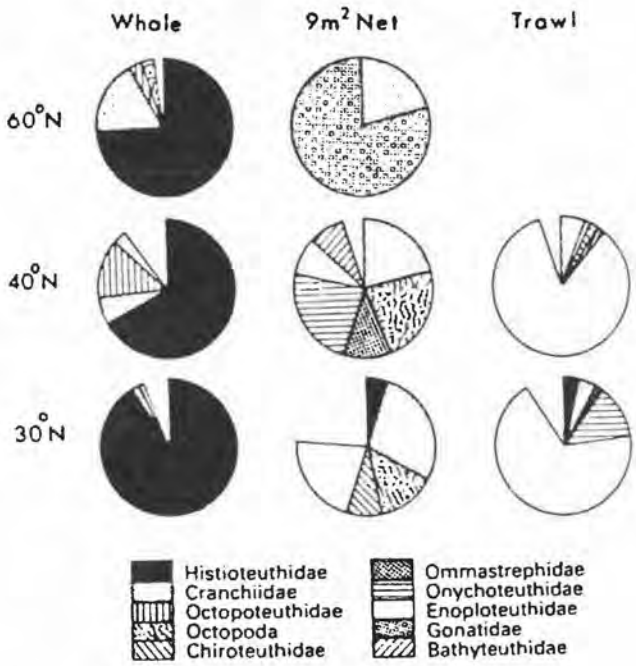


Table 9. Estimate of the total biomass of squids eaten by some predators in the Antarctic. (From M. Clarke, 1983).

	Stock Size (1000s)	Mean Individual wt (kg)	Stock Weight (1000 mt)	Percent squid in diet	Percent body weight eaten/day	Number of predator days/year	Total squid eaten/year (mt X 10^6)
Sperm whale	85	40.0	3400	95	3	122	11.8
Total baleen whales	975	-	43125	1?	3.5	122	1.8
Elephant seal	600	500.0	300	75	6	333	4.5
Crabeater seal	15000	193.0	2868	2	7	335	1.345
Ross seal	220	173.0	38	64	7	335	0.571
Weddell seal	730	246.0	180	11	7	335	0.463
Fur seal	200	50.0	10	33	7	335	0.077
Leopard seal	220	272.0	60	8	7	335	0.112
Total seals							7.07
Wandering albatross	70	9.0	0.63	80	7	365	0.013
Grey-headed albatross	385	3.6	1.39	49	7	365	0.017
Black-browed albatross	12000	3.5	42.00	21	7	365	0.225
Total albatrosses	12630	-	44.45	30?	7	365	0.34
All birds	350000	2.4	850.00	24	7	365	13.54
Total estimate							34.21

compared to the estimated annual krill consumption of Antarctic baleen whales (approximately 34 million tons; Table 40, this paper) and seals (approximately 146 million tons); Table 33, this paper), the potential importance of cephalopods as predators is apparent.

Virtually nothing is known of squid feeding behavior in the Southern Ocean. McSweeny (1978) reported that stomach contents of Galiteuthis glacialis were composed of relatively large pieces of food. This observation supports the view of Bidder (1966) that cephalopods bite and swallow their prey rather than chew.

The work of Karpov and Cailliet (1978), studying Loligo opalescens in California, may provide some insight into some factors affecting prey composition and feeding behavior that may be operative in Antarctica. They found that in California, prey composition: 1) is dependent on squid size; large squid feed mainly on euphausiids, cephalopods, and fish; small squid feed mainly on crustaceans, such as megalops larvae and cumaceans (Table 10), 2) is dependent on depth of feeding, 3) is largely independent of predator sex, and 4) differs between spawning grounds and shallow water areas.

Importance to Predators

Squid constitute a significant portion of the diets of Antarctic organisms. Sperm whales, Commerson's dolphins, killer whales, Weddell seals, Ross seals, elephant seals, penguins, albatrosses, and larger cephalopods are all reported to prey on squid (M. Clarke, 1983). Many predators feed entirely on squid and many more include squid in their diet (SCAR/SCOR, 1983a). In marine systems where the role of cephalopods is better understood (e.g., off the California coast) squid are important prey for a wide variety of vertebrate predators (Morejohn et al., 1978).

In Antarctica, the bulk constituent (76%) of sperm whales' diet consists of the cranchiid squid (which grows to 10 m in length). This species has only been caught in nets once (M. Clarke, 1983). Second most important in sperm whales' diet are the onychoteuthids (M. Clarke, 1983).

Cephalopods are also an important prey item for elephant seals which eat fish and squid almost exclusively (Laws, 1960a; King, 1964). Stomach contents from elephant seals at Signy Island, South Orkney Islands, showed that, by number, Gonatus antarcticus, an unidentified teuthoid, Morotheuthis knipovitchi, and an octopod comprised 42%, 20%, 14%, and 10%, respectively of the total prey taken. By weight, the octopod, Gonatus antarcticus, and Moroteuthis knipovitchi contributed 60%, 15%, and 10%, respectively (Clarke and MacLeod, 1982a).

Weddell seals readily prey on cephalopods when they are available (Bertram, 1940). Lipinski and Woyciechowski (1981), studying Weddell seals at Admiralty Bay, found that in stomachs containing food, 92% contained cephalopods. Clarke and Macleod (1982) examined the stomach contents of Weddell seals from Deception Island, South Shetland Islands.

Table 10. Index of relative importance in prey by size and habitat eaten by Loligo opalescens off California. (From Karpov and Cailliet, 1978).

	Squid Size		Sample Location		
	Small	Large	Deep water	Shallow water	Spawning grounds
Number of Squid	123	103	134	94	52
Crustacea unknown	73.3	17.5	23.8	135.2	95.4
Euphausiacea	3988.0	5400.0	6552.2	1553.4	0.0
Copepoda	97.5	37.5	103.8	1.0	0.0
Mysidacea	7.4	10.6	6.3	28.2	54.7
Megalops	4.9	0.0	0.1	23.3	1088.0
Natantia	0.2	0.6	0.0	1.9	0.0
Cumacea	12.2	0.0	2.6	1.0	0.0
Amphipoda	0.0	0.1	0.1	0.0	11.3
Ostracoda	0.0	0.1	0.1	0.0	0.0
Cephalopoda (whole)	16.2	9.7	2.6	187.6	0.0
Gastropoda	5.0	1.2	1.9	5.7	295.8
Radiolaria	0.0	0.4	0.1	1.0	0.0
Polychaeta	0.0	0.0	0.0	0.0	24.9
Fish	2.0	8.8	1.3	44.8	11.3
Miscellaneous	-	-	-	-	197.2

The squids, Moroteuthis knipovitchi and Psychroteuthis glacialis, represented 31.3% and 28.7% by number, respectively, of the cephalopods found. By weight, Moroteuthis knipovitchi comprised 48.5% of cephalopods present.

Although many cephalopods taken by birds may have a lower caloric value than other prey such as fish and krill (Croxall and Prince, 1982), squids represent important prey items for seabirds. At South Georgia, 50% of the grey-headed albatross diet consists of squid. Of that 50%, the dominant portions were Todarodes and Mesonychoteuthis (88% and 8% by number; 91% and 4% by weight) (Clarke and Prince, 1981a). In the black-browed albatross, 21% of the diet consists of squid. Likewise, the dominant species are Todarodes and Mesonychoteuthis (68% and 25% by number; 76% and 12% by weight) (Clarke and Prince, 1981a). Wandering albatrosses at South Georgia are known to feed on larger species of squid than they would otherwise be expected to utilize. The albatrosses presumably gain access to these larger squid such as Taningia and Kondakovia by feeding on the vomit of sperm whales at sea (Clarke et al., 1981b).

CHAPTER 5: ANTARCTIC FISH

Introduction

In most of the world's oceans the fish fauna has been the subject of special interest and study due to its economic importance. However, interest in Antarctic fisheries is a relatively recent phenomenon. Since the mid-1960's, when commercial fishing in the Southern Ocean began, various nationalities have visited Antarctic waters annually. Research efforts have also increased, leading to a better understanding of Antarctic fish biology. Major reviews of this body of literature include those by Marshall (1964), Andriashev (1965), DeWitt (1971), Kock (1975), Permitin (1977), and Everson (1977, 1981, 1984b). Physiology, biochemistry, and genetic aspects were briefly discussed by A. Clarke (1983). This chapter draws on this foundation and especially literature published since 1977.

Species Composition

Approximately 120 species of fish, excluding bathypelagic and bathydemersal species, have been found south of the Antarctic Convergence. The dominant group of Antarctic fish is Notheniiformes, a group comprising five families, over 70% of all coastal species, and 90% of all individuals (DeWitt, 1971; Everson, 1977; Iwami and Abe, 1981). The five families that comprise the Notothenioidei are Nototheniidae (Antarctic cods), Channichthyidae (ice fishes), Harpagiferidae (plunder fishes), Bathydraconidae (dragon fishes), and Bovichthyidae. The Nototheniidae and Channichthyidae represent the major Antarctic fish species of potential commercial importance. The Notothenioid fish are mostly sedentary, demersal species (DeWitt, 1971; DeWitt and Hureau, 1979), although some have adapted to living closely associated with the underside of sea ice such as Pagotheria borchgrevinski (DeVries, 1978). The remaining major groups of Antarctic fish include Myxinidae, Bothidae, Gadidae, and Rajidae. Some species of these last two families are of potential commercial importance (Table 11). The Myctophidae and other bathypelagic groups have not been included in Table 11, because although they may well be abundant in the open oceans, they do not form concentrations, and in the past have not supported viable fisheries. However, a catch of approximately 500 metric tons of Mictophid fish was reported for the 1982/83 season (Duhamel, pers. comm.).

Two further features characterize the Antarctic fish fauna. First, the Southern Ocean lacks shoaling species of obligate pelagic fish, which is surprising in view of the availability of Antarctic krill (as a potential food source. The second feature is the relatively high numbers of endemic fish species found around many of the Antarctic and sub-Antarctic Islands (DeWitt, 1971).

Table 11. Some common and potential commercially important fish species in the Southern Ocean (* not commercially fished but commonly caught).

GROUP	FISH SPECIES	COMMON NAME
RAJIDAE	Raja georgiana	
	Raja murrayi	Rays
	Raja eatonii	
GADIDAE	Micromesistius australis	Southern poutassou or blue whiting
NOTOTHENIIDAE	Notothenia gibberifrons	Bumphead notothenia
	Notothenia rossii rossii	
	Notothenia rossii marmorata	Marbled notothenia
	Notothenia magellanica	
	Notothenia squamifrons	Scaled notothenia
	Notothenia nudifrons	Nakedhead notothenia
	Notothenia guentheri	Guenther's notothenia
	*Notothenia coriiceps coriiceps	
	*Notothenia coriiceps neglecta	
	*Notothenia kempi	
	*Notothenia larseni	
	*Notothenia angustifrons	
	*Trematomus bernacchii	
	*Trematomus hansoni	
	Dissostichus mawsoni	Antarctic toothfish
	Dissostichus eleginoides	Patagonian toothfish
	Pleuragramma antarcticum	Antarctic sidestripe or Antarctic silverfish
CHANNICHTHYIDAE	Champsocephalus gunnari	Antarctic icefish
	Channichthys rhinoceratus	Longsnouted icefish
	Pseudochaenichthys georgianus	South Georgia icefish
	Chaenocephalus aceratus	Scotia Sea icefish
	Chionodraco restrospinosis	Kathleen's icefish
	Chaenodraco wilsoni	Wilson's icefish

Distribution

Zoogeography

The bottom-dwelling, perciform stock of Antarctic fishes evolved to occupy various types of Antarctic habitat (Regan, 1914; Norman, 1938; DeWitt, 1971; Targett, 1981) (Table 12). This diversity occurred as Antarctic fish acquired the physiological specialization necessary for survival in subzero seawater temperatures (DeVries and Eastman, 1981). Moreover, low water temperatures, extreme geographical isolation, and lack of south-flowing surface currents prevented most other fish groups from becoming established in Antarctic shelf waters. As a result, non-Notothenioid fishes constitute less than 10% of individuals overall, and as little as 1% of the fish fauna in some areas such as the Ross Sea (DeWitt, 1971).

Many fish species inhabit the shelf waters surrounding major islands, seamounts, and continent (Tables 12 and 13). This distinction has resulted in a high degree of endemism among shallow-water species. DeWitt (1971) noted that 95% of the Notothenioids and nearly 70% of the non-Notothenioid fish (comprising about 25% of Antarctic coastal fish species) are endemic to the Antarctic region (see also Targett, 1981). However, the degree of endemism varies greatly within Antarctic waters. Iwami and Abe (1982) compared the Channichthyid fauna of the South Shetland Islands and the Ross Sea area and found that in western Antarctica, 87% of the Channichthyids were endemic whereas only 7% were endemic to east Antarctica. Endemism is far less pronounced in the deep-water fish fauna where only about half the species are restricted to the Antarctic Zone (DeWitt, 1971).

In a recent study of eastern Antarctic fish (Bouvet to Kerguelen Islands) Duhamel et al. (1983) drew some useful ecological conclusions relating fish abundance, zoogeography, and habitat. They suggested that the fish distribution in the area studied is influenced mainly by two factors: the position of the Antarctic Convergence, which separates Marion and Crozet Islands from Bouvet Island; and the biogeographical transition zone between western and eastern Antarctic waters. They noted that Channichthyidae were absent around Marion and Crozet Islands but present around Bouvet, Kerguelen, and Heard Islands. Thus, Channichthyidae (especially Champsocephalus gunnari) represent a useful index of the presence of cold water masses situated south or nearby the Antarctic Convergence, a highly productive zone directly related to fish abundance.

Stock discreteness

In his review of coastal and deep water fish of the Antarctic, DeWitt (1971) concluded that many species occurring near the Continent had a circumpolar distribution. He also confirmed the 'transitional' species composition along the Scotia Arc, suggesting that the fish of the

Table 12. Gross distribution of some common and commercially important Antarctic fish species, (+ inferred distribution but no evidence; X gross distribution based on literature). (From Ciechomski and Weiss, 1974).

FISH SPECIES \ LOCATIONS	Antarctic Peninsula	South Shetland Islands	South Orkney Islands	South Sandwich Islands	South Georgia (including Shag Rocks)	Bouvet Island	Crozet Island	Kerguelen Island	Heard Island	Macquarie Island	Marion/Prince Edward Islands
Raja georgiana	+	+	+		X						
Raja murrayi								X			
Raja eatonii								X	X		
Micromesistius australis		X	X		X					X	
Electrona antarctica	X	X	X	X	X	X					
Notothenia gibberifrons	X	X	X	X	X						
Notothenia rossii rossii							X	X	X	X	X
Notothenia rossii marmorata	X	X	X	X	X						
Notothenia magellanica		X	X	X	X		X	X	X	X	
Notothenia squamifrons		X	X		X	X	X	X	X		X
Notothenia nudifrons	X	X	X	X	X						
Notothenia coriiceps coriiceps							X	X	X		X
Notothenia coriiceps neglecta	X	X	X	X	X	X					
Notothenia kempi	X	X	X	X	X						
Notothenia larseni	X	X	X	X	X	X	X				X
Notothenia angustifrons				X	X						
Trematomus bernacchii	X	X	X		X						
Trematomus hansoni	X	X			X						
Dissostichus mawsoni	X	X									
Dissostichus eleginoides		X	X		X	X	X	X	X		X
Pleuragramma antarcticum	X	X	X								
Champsocephalus gunnari	X	X	X	X	X	X		X	X		
Channichthys rhinoceratus								X	X		
Pseudochaenichthys georgianus	X	X	X	X	X						
Chaenocephalus aceratus	X	X	X	X	X	X					
Chionodraco restrospinosus	X	X	X								
Chaenodraco wilsoni	X	X	X								
Pseudochaenichthys georgianus				+	X						
Parachaenichthys charcoti	X	X	X								

Table 13. Biological information for selected species of Antarctic fish. (Modified from Permitin, 1973).

SPECIES OF FISH	STAGE	ECOTYPE	DISTRIBUTION	DEPTH (m)	PREFERRED HABITAT
Raja georgiana	juv.+adult	demersal	shelf	180 - 830	mud
R. murrayii	juv.+adult	demersal	shelf	20 - 60	---
R. eatonii	juv.+adult	demersal	shelf	30	---
Micromesistius australis	juv.+adult	mostly pelagic	shelf	10 - 650	open water
Notothenia gibberifrons	juv.+adult	demersal	shelf	3 - 500	mud
N. coriiceps coriiceps	juv.+adult	demersal	shelf nearshore	0 - 200	rock, sand, mud, algae
N. coriiceps neglecta	juv.+adult	demersal	shelf nearshore	0 - 200	rock, sand, mud, algae
N. rossii rossii	juvenile	demersal	shelf nearshore	0 - 30	macroalgae beds
N. rossii rossii	adult	demerso-pelagic	shelf offshore	30 - 450	mud/open water
N. rossii marmorata	juvenile	demersal	shelf nearshore	1 - 90	macroalgae cover
N. rossii marmorata	adult	demerso-pelagic	shelf offshore	90 - 350	mud/open water
N. magellanica	juv.+adult	demerso-pelagic	oceanic	0 - 80	mesopelagic
N. squamifrons	adult	demersal	shelf	10 - 600	mostly on mud at 200 - 300m depth
N. nudifrons	juv.+adult	demersal	shelf	3 - 400	varies with depth and found mostly 4 - 128m
N. kempi	juv.+adult	demersal	shelf	100 - 355	mud/open water
N. larseni	juv.+adult	demerso-pelagic	shelf	90 - 400	mud/open water mostly
N. angustifrons	juv.+adult	demersal	shelf nearshore	1 - 30	mud, sand rock, algae
Trematomus bernacchii	juv.+adult	demersal	shelf nearshore	5 - 200	mud, sand, rock, algae
T. hansoni	juv.+adult	demerso-pelagic	shelf	5 - 650	varies with depth but on mud at 90 - 240m
Dissostichus mawsoni	juv.+adult	mostly pelagic	mainly oceanic	20 - 400	open water
D. eleginoides	juv.+adult	mostly pelagic	shelf/slope	150 -1500	open water
Pleuragramma antarcticum	juv.+adult	pelagic	mainly oceanic	1 - 730	open water mostly at depths of 310 - 355m
Champsocephalus gunnari	adult	demerso-pelagic	shelf	0 - 450	mud/open water
Pseudochaenichthys georgianus	juv.+adult	demerso-pelagic	shelf	0 - 500	mud
Chaenocephalus aceratus	juv.+adult	demerso-pelagic	shelf	1 - 240	mud
Chionodraco sp.	juv.+adult	demersal	shelf	0 - 800	varies with depth

isolated islands further east were derived from the ichthyofauna of the Scotia Arc Islands. Duhamel et al. (1983) described similarities in the Chaenocephalus aceratus populations at Bouvet Island and western Antarctica. Whereas the existence of separate Antarctic fish stocks is poorly known for many species, there is some evidence that discrete stocks occur.

For example, distinct stocks of Micromesistius australis have been isolated in the Southern Ocean (Inada and Nakamura, 1975; Shpak, 1975). Antarctic fish for which there is evidence of more than one discrete management stock are listed in Table 14. Freytag (1980) described separate stocks of Notothenia rossii marmorata stocks from South Georgia, the South Shetland Islands, and the South Orkney Islands based on differences in growth, parasites, and phenotypic. However, Burchett (1983a) noted that phenotypic variations within populations at South Georgia were often greater than variations between populations from different locations.

Similarly, identifying stocks by differences in growth can be misleading. These differences may not be attributable directly to genotypic variation but to variation in the physical environment (Burchett, 1983a). Under identical environmental conditions, fish taken from different geographical locations may develop and grow at the same rate.

Mark-recapture studies may provide reliable evidence of stock separation within subspecies. Whereas Duhamel (1982) reported evidence of migration for Notothenia rossii at Kerguelen, Burchett (1983a) found that adults of this species at South Georgia do not migrate away from the shelf area of the Island. However their larvae are widely dispersed throughout the Scotia Sea. Given the direction and strength of the surface currents along the Scotia Arc (Hall, 1974), distribution of larvae and fingerlings in a northeast direction is likely to occur. Thus, although adult fish stocks may be distinct, genetic exchange may result from dispersal of immature stages, especially during summer and autumn. Exchange of fish along the Scotia Arc by surface currents has been suggested by DeWitt (1971).

Parasites and genetics have been used as "tags" in determining stock separation. Siegel (1980), using "parasitic tags", and Kock (1981) concluded that there were distinct stocks of Chaenocephalus aceratus and four separate populations in the Scotia Arc area (at South Georgia, South Orkney Islands, Elephant Island, and South Shetland Islands). Sosinski (1981) presented some evidence for discrete stocks of Champsocephalus gunnari, but pointed out that local stocks may well migrate between individual fishing grounds. Recent work on species separation using "genetic tags" in Notothenioid fish has demonstrated the potential utility of this method in stock separation studies (Anderson, 1982). The results of these electrophoretic analyses appear promising. The coefficients of genetic distance substantially supported the conclusions of conventional taxonomy.

Table 14. Antarctic fish species for which there is evidence for more than one discrete management stock.

Micromesistius australis	a)	Scotia Sea, probably southern limit of Patagonian population	
	b)	Campbell Plateau.	
	a)+b)	Related subspecies on morphological grounds.	Inada and Nakamura (1975)
	a)+b)	Not considered of subspecific status but isolated.	Shpak (1975)
	c)	Southern Scotia Sea around South Orkney Islands and South Shetland Islands.	Shubnikov et al. (1969)
	d)	North and south of the Antarctic Convergence.	Shust (1978)
Notothenia rossii	a)	Kerguelen/Crozet groups considered of subspecies status i.e. *N. rossii rossii*	Nybelin (1947)
	b)	Scotia Arc groups considered to be of subspecific status ie. *N. rossii marmorata*.	Nybelin (1947)
	c)	Distinct stocks of *N. rossii marmorata* occur along the Scotia Arc Islands.	Freytag (1980)
	d)	Distinct stocks of *N. rossii marmorata* are present at least at adult stage but with genetic exchange of larvae and fingerlings from further south along the Scotia Arc.	Burchett (1983a)
Champsocephalus gunnari		Differentiation of stocks from northern fishing grounds of Atlantic sector (South Georgia and Shag Rocks) and specimens from southern grounds (South Orkney Islands, South Shetland Islands and Elephant Island.	Sosinski (1981)
Chaenocephalus aceratus		Distinct stocks from South Georgia, South Orkney Islands and South Shetland Islands.	Siegel (1980)

Abundance

Determining the abundance of Antarctic fish stocks has been the focus of increasing efforts in recent years. Kock et al. (1984) reviewed the status of exploited fish stocks and noted that biomass has been estimated with two methods: 1) production estimates (as utilized by Everson, 1977, 1984b), and 2) "swept area" methods (as utilized by Hureau, 1980; Kock, 1980, 1981, 1984b).

Several trawl surveys were carried out near South Georgia (reported to the second meeting of the BIOMASS Working Party on Fish Biology) and in the vicinity of Kerguelen (Hureau, 1980). The total fish stock around Kerguelen was estimated by Hureau at approximately 130,000 tons.

Estimates of fish production have been calculated from presumed levels of consumption of fish by predators. Everson (1984b) estimated that whales consume about 1129 x 10^3 tons, seals 7685 x 10^3 tons, and birds 6750 x 10^3 tons per annum, for a total annual fish consumption of 15,564 x 10^3 tons. The demersal fish (which make up over 90% of the fish population in the 0-1000m depth zone) are, for the most part, restricted to the continental and island shelves which together cover an area of about 2.2 million km^2 (excluding ice shelves; Everson, 1977). The total consumption of fish, if averaged over the whole shelf area is therefore about 7.1 tons/km^2. This estimated production of fish is quite close to that derived for Notothenia neglecta at Signy by Everson (1970a). However, that estimate may be innaccurate as no account has been taken of fish consumed by other fish. Other fish are an important component of the diets of many common fish species such as Chaenocephalus aceratus, Notothenia rossii, and Champsocephalus gunneri.

A concise summary of the development of Antarctic fish exploitation is provided by Kock et al. (1984). Heavy fishing has been undertaken since the late 1960's; principally in the Atlantic Sector. Commercially important species include Notothenia rossii, N. guntheri, and Champsocephalus gunnari. The potential impact that fisheries have had on Antarctic fish stocks has been discussed by several authors (Everson, 1977, 1984b; Gulland, 1982; Burchett and Ricketts, 1984). It is likely that fishing pressure may have led to locally depressed stocks of Antarctic fish. Careful consideration must be given to managing those stocks that may have been too heavily fished in the past as well as those stocks likely to be heavily exploited in the future.

Size and Growth

Most Antarctic fish are relatively small, with fewer than half reaching 25 cm in length and only about 12 species growing to more than 50 cm in length (Andriashev, 1965). There are, however, large species such as Dissostichus mawsoni, which attains a weight of 77 kg, a length of 165 cm (Raymond, 1975), and an age of 31 years (Burchett et al., 1984). Dissostichus eleginoides reaches a weight of 52 kg, a length of 186 cm, and an age of 22 years (Zacharov and Frolkina, 1976; Kock, 1980c).

Antarctic fish, in general, have slow, seasonal growth patterns (Everson, 1970a, 1984b; DeVries and Eastman, 1981; Burchett, 1983b), and low metabolic rates (A. Clarke, 1983). Everson (1984b) reported that fish in higher latitudes do grow more slowly than temperate water species and at about the same rate as those from other cold regions.

The life history strategies of many polar organisms are characterized by slow growth, delayed maturity, and the production of relatively precocious young. Growth data summarized by DeVries and Eastman (1981) indicate that many of the Antarctic fish do indeed have slow metabolisms and growth rates.

Growth cycles

Seasonal variation in condition is influenced by cycles of gonad maturation, fish activity, feeding, and energy stores. Hureau (1970) compared changes in condition for six species of Antarctic fish. He found that although condition generally decreased with increasing age (with the exception of Trematomus hansoni and Trematomus bernacchii), there was no clear seasonal cycle beyond the gonad cycle. However, Everson (1970a, 1970b) found a distinct seasonal cycle in Notothenia neglecta at Signy Island. During the months prior to spawning, condition reaches a peak and then declines to a post-spawning level. Moreover, there is a slight increase in condition at mid-winter, a further decline in spring, and a summer increase prior to spawning.

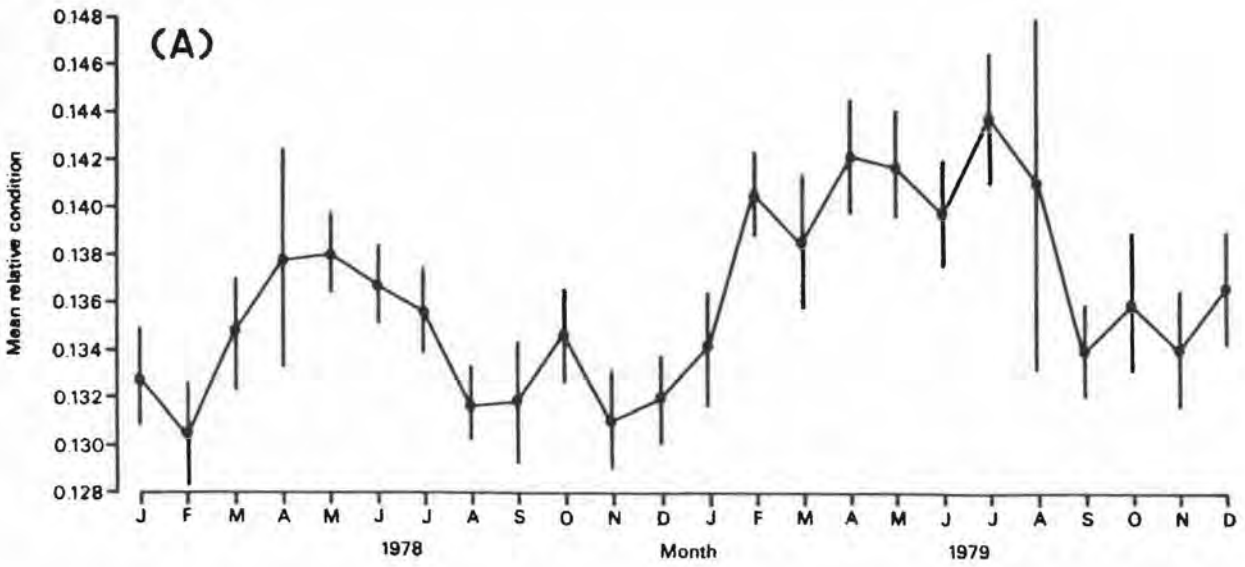
Burchett (1983b) studied the annual growth cycles (condition and relative liver size) of the young (fjord) stages of Notothenia rossii at South Georgia (Figure 13). The condition index increased in late summer (April onward) and declined steadily throughout the late winter (July to December). The mean weight of juvenile fish was also greatest in summer (February). These data suggest that most growth in young Notothenia rossii occurs in summer months. Peak relative liver size normally occurs approximately two months later than the peak relative condition. The liver is probably being used as an energy store, allowing the fish to build up reserves in late summer when they have been feeding intensively. In winter months these reserves could be utilized gradually when food is scarcer.

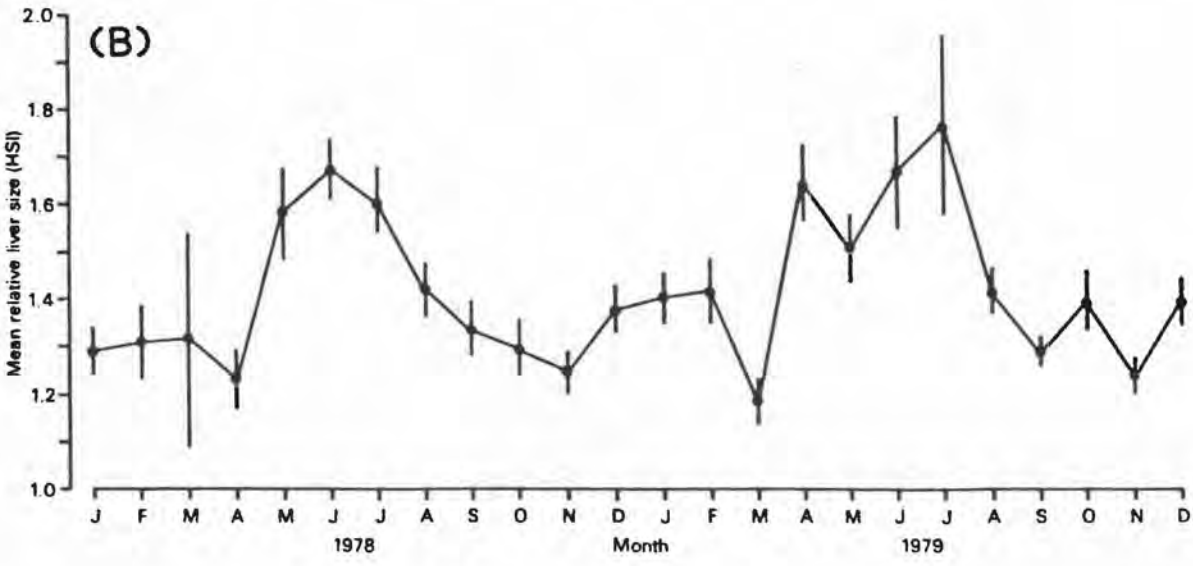
Reproduction

Age at sexual maturity

As a consequence of the slow growth rates, the slow metabolic rates, and the relatively long life spans of most Antarctic fish, many do not reach sexual maturity until 3 to 8 years of age (Table 15). Age at sexual maturity also varies between the sexes. Male Notothenia neglecta (Everson, 1970b), N. rossii marmorata (Olsen, 1954; Shust, 1978), N. rossii (Hureau, 1970), and Chaenocephalus aceratus (Kock, 1981) mature approximately one year earlier than females. However, in other species

Fig. 13. (A) Annual variation of mean relative condition of juvenile Notothenia rossii sampled nearshore at South Georgia during 1978 and 1979. Vertical bars represent 95% confidence limits. (B) Annual variation of mean relative liver size (HSI) of juvenile Notothenia rossii sampled nearshore at South Georgia during 1978 and 1979. Vertical bars represent 95% confidence limits of the mean.





such as Notothenia kempi (Shust, 1978), N. squamifrons (Duhamel and Hureau, 1981), Champsocephalus gunnari, and Pseudochaenichthys georgianus (Kock, 1981), both sexes mature at the same age. There is no apparent evidence suggesting that differential maturation occurs within species from different locations or latitudes.

Gonad maturation and development

The development and final maturation of the gonads for several species of Antarctic fish were described by Dearborn (1965), Everson (1970b) and Hureau (1970). Subjective maturation stages based on Notothenia neglecta and applicable to most Nototheniiformes were outlined by Everson (1977) (Figure 14). Everson (1970b) described the following reproductive pattern as typical for Nototheniid fish. After spawning, the fish ovaries remain more or less constant in size, representing about 3% of body weight during the next 6 months (stages 5 and 6). Between 6 and 10 months after spawning there is a gradual increase in ovary size, followed by a rapid 2-month increase when the ovary doubles in size (stage 4). This period culminates in spawning. The reduction in ovary size at spawning does not leave the ovary totally devoid of ova; many small ova are present which will form the next years' eggs

The maturation of testes also show an annual cycle. However, rather than a rapid increase in size, there is a steady rise for the 6 months preceeding spawning. Spawning is followed by a reduction in testis size due to release and re-absorption of sperm.

Although the final maturation processes in most species of Antarctic fish are more or less synchronized, there is evidence of slight variations in timing related to intraspecific size differences. One of the better examples is that of Notothenia cyanobrancha from Kerguelen Island, where fish spawning for the first time do so at the end of January, prior to the peak spawning period for the remainder of the population (which spawn at the end of April) (Hureau, 1970). Everson (1970b) found a similar situation for the Notothenia neglecta population at Signy Island (South Orkney Islands) where final maturation and spawning by females of the smallest mature size group occurred about a month earlier than the rest of the population. An opposite pattern may occur in some of the species of Channichthyidae. The average dry egg weight of Champsocephalus gunnari in pre-spawning condition is greatest in largest fish, indicating either that final maturation occurs earlier in older fish, or that larger fish tend to produce larger eggs (Kock, 1979, 1981).

Ova development and fecundity

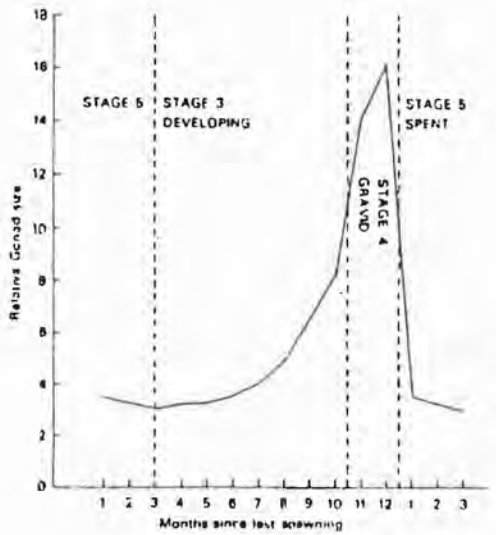
Early studies by Marshall (1953) concluded that Antarctic fish produce relatively few, large, yolky eggs, and larvae which hatch at an advanced stage. Eggs range in size from 0.7 mm for Muraenolepis microps to 4.8 mm for Notothenia rossii marmorata, with an average egg size of 2.8 mm.

Table 15. Age and size at sexual maturity for selected specis of Antarctic fish (F=Female; M=Male; B=Both; (min.)=minimum; Av.= average).

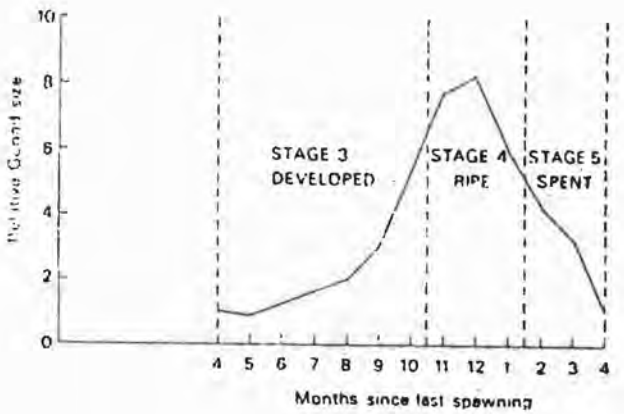
SPECIES OF FISH	LOCATION	SEX	AGE	LENGTH (mm)	WEIGHT (g)	REF
Raja georgiana	South Georgia	F		600		24
Micromesistius australis	Scotia Sea	M	4	453		25
M. australis	Scotia Sea	F	3	464		25
Notothenia gibberifrons	Scotia Sea	F		350	400	4
Notothenia coriiceps negl.	South Orkneys	M	8	300		6,26
N. c. neglecta	South Orkneys	F	7	290		6,26
N. c. neglecta	Terre Adelie	M	7	180	190	7
N. c. neglecta	Terre Adelie	F	8	225	130	7
Notothenia rossii rossii	Kerguelen	M	7	480	1700	7
N. rossii rossii	Kerguelen	F	8	550	2700	7
N. rossii rossii	Kerguelen	B	7 - 8			9
N. rossii marmorata	South Georgia	M	5 (min.)	400		27
N. rossii marmorata	South Georgia	F	6 (min.)	450		27
N. rossii marmorata	South Georgia	M	4 - 5	350 - 400		28
N. rossii marmorata	South Georgia	F	5 - 6	400 - 450		28
Notothenia magellanica	Kerguelen	B	6 - 7	250	500	7
Notothenia kempi	South Georgia	B	4 (min.)			28
Notothenia squamifrons	Kerguelen	M	5 - 6			9
N. squamifrons	Kerguelen	F	5 - 6			9
D. eleginoides	South Georgia	F		550 - 600		13
D. eleginoides	Kerguelen	B	7			9
Champsocephalus gunnari	South Georgia	B	4			22
C. gunnari	South Gerogia	M	4	210 - 260		3
C. gunnari	South Georgia	F	4	210 - 250		3
C. gunnari	South Georgia	F	3 - 4	200 - 270		20
C. gunnari	Kerguelen	F	3 - 4	260 (min.)		20
C. gunnari	South Scotia Sea	F		Av. 320		20
C. gunnari	South Georgia	B	3 - 4	210 - 260		18,29
C. gunnari	Kerguelen	B	3	240-250		9
Chaenocephalus aceratus	South Gerogia	B	6 - 7	440 - 715		18
Channichthys rhinoceratus	Kerguelen	B	5	340	435	9
C. rhinoceratus	Kerguelen	B	5			9
Pseudochaenichthys georgianus	South Georgia	M	4 - 6	400 - 480		3
Ps. georgianus	South Georia	F	4 - 6	440 - 500		3
Chionodraco sp.	Scotia Sea	M		310 - 360		3
Chionodraco sp.	Scotia Sea	F		330 - 370		3

Table references: 1. Hart (1946), Weiss (1974); 2. Ciechomski and Weiss (1974); Permitin (1973); 4. Permitin and Silyanova (1971); 5. Lisovenko and Silyanova (1979); 6. Everson (1970b); 7. Hureau (1970); 8. Burchett et al. (1983); 9. Duhamel and Hureau (1981); 10. Linkowski and Rembiszewski (1978); 11. Chojnacki and Palczweski (1981); 12. Andriashev et al. (1979); 13. Hureau and Ozouf-Costaz (1980); 14. Duhamel (1981); 15. Zacharov and Frolkina (1976); 16. Everson (in press); 17 Yukhov (1971); 18. Kock (1979); 19. Kock (1980a); 20. Sosinski (1979); 21. Kompowski (1980b); 22. Olsen (1955); 23. Hureau (1966); 24. Permitin (1969); 25. Shubnikov et al. (1969); 26. Everson (1970a); 27. Olsen (1954); 28. Shust (1978); 29. Kock (1980b).

Fig. 14. (A) Probable seasonal pattern of relative female gonad size (gonad weight/total weight) x 100. Morphological characteristics of stages: (1) Immature - ovary small, firm; no ova visible to naked eye. (2) Maturing virgin - ovary length body cavity, firm, full of eggs. (3) Developing - ovary large, contains eggs of two sizes. (4) Gravid - ovary large; when opened large ova spill out. (5) Spent - ovary flaccid, contains few large and many small ova. (B) Probable seasonal pattern of relative male gonad size. Morphological characteristics of stages: (1) Immature - testis small, translucent. (2) Developing - testis small, white, convoluted. (3) Developed - testis large, white, convoluted; no milt produced when cut. (4) Ripe - testis large, opalescent white; milt produced when cut. (5) Spent - testis smaller, dirty white in color. (After Everson, 1977).



(A)



(B)

Recent studies of Notothenia neglecta indicate that due to the large size of ova, yolk deposition may take more than one year (Everson, 1970b). In the years before females become fully mature, the ovary slowly develops to a length of one quarter of the body cavity. The ova at this stage are about 0.5 mm in diameter. At maturity these ova enlarge and increase in yolk volume; simultaneously yolk deposition begins in a new generation of ova. There are thus two distinct size classes of yolky oocytes present in a mature ovary. Yolk deposition probably continues throughout most of the year in both types of oocytes, although the greatest increase occurs in the largest ova immediately prior to spawning.

A biennial process of ova maturation probably also occurs in Trematomus bernacchii where spent ovaries containing eggs of about 1 mm in diameter have been observed (Hureau, 1964). Biennial maturation has been confirmed by Andriashev et al. (1979) for Trematomus bernacchii and Pagothenia borchgrevinki from the Davis Sea ($66^{\circ}S$). Kock (1979) reported that biennial ova maturation also takes place in Champsocephalus gunnari, Chaenocephalus aceratus, and Pseudochaenichthys georgianus.

The relative fecundity (i.e., number of eggs consituting one season's spawn divided by total weight of fish) is low and varies markedly between fish of different species and localities. There is an inverse correlation between egg size and relative fecundity, and in general it appears true to say that for fish of the same size, eggs are larger in fish from higher latitudes (Permitin and Silyanova, 1971). Kock (1981) found relative fecundity to be highest in those individual Champsocephalus gunnari, Pseudochaenichthys georgianus, and Chaenocephalus aceratus that were spawning for the first time. Relative fecundity decreased in Champsocephalus gunnari but increased in Chaenocephalus aceratus with increasing latitude.

Spawning period

Spawning timing appears to differ slightly both interspecifically and intraspecifically depending upon the size of fish and the geographic latitude. Of the 24 species of Antarctic fish for which spawning periods are known, 30% of all individuals spawn in summer, 43% in autumn, 17% in winter, and 10% in spring (Tables 16 and 17). Approximately 71% of species spawn in late summer and autumn (March to June), with peak spawning occurring around May-June (54%). Only 29% of species spawn during the 8 months of the year between July and February. Although duration of spawning differs markedly between species (Fig. 15), those species breeding in summer (January to April), especially in early summer (February), have a longer spawning period than fish spawning in autumn and winter. Species spawning between January and April have an average spawning period of over 61 days while those spawning from May to December have an average spawning period of 48 days.

Although most Antarctic fish, with the exceptions of Notothenia magellanica (Hureau, 1970) and possibly Pleuragramma antarcticum (a truly pelagic species), lay demersal eggs, recent research has indicated some interesting exceptions. White et al. (1982) found that Notothenia neglecta embryos at Signy Island (South Orkney Islands) became negatively bouyant after 14 days, while those from South Georgia floated throughout the whole period of embryo development. Knowing whether eggs and developing embryos normally float throughout development or rapidly become negatively bouyant before or after fertilization is important for assessing the distribution of populations.

Hatching period and larval development

Although the spawning season for most species is relatively short, the time lapse between spawning and emergence of larvae is considerable (Burchett et al., 1983). Burchett et al. (1983) found that the time between first spawning and first hatching was found to vary from 60 days in Notothenia squamifrons to 270 days in Chionodraco sp. However, this difference may be somewhat misleading because hatching primarily occurs in late winter and spring (August to October), regardless of spawning timing. Fish spawning in spring and early summer have a short embryonic period, hatching at the end of summer (Efremenko, 1983).

On the basis of lengths at hatching for 25 Antarctic fish species (Table 17) it was estimated that larval hatching size varied from 4.5 mm in Gymnoscopelus braueri to 18.5 mm in Pseudochaenichthys georgianus (with a mean larval hatching length for all Antarctic fish of 11 mm). However, based on egg sizes (Burchett, 1983b), larvae lengths were smaller, ranging from 2.2 mm in Muraenolepis microps to 15.1 for Notothenia rossii marmorata (with an overall average of 8.5 mm for the Antarctic fish). The average hatching length of Antarctic fish is about 10 mm, which agrees with the findings of Marshall (1953), Everson (1970b), North and White (1982), and Efremenko (1983) that larvae are hatched at a large size and an advanced stage.

Even though recently hatched larvae are large, and will sometimes prey on Euphausiids (e.g., Channichthyids) most larvae are able to feed on only the smallest zooplankton, primarily copepod larvae (Daniels, 1979; Hoshiai and Tanimura, 1981; Burchett, 1983c). Because copepod larvae are most abundant immediately following the commencement of the spring and summer phytoplankton blooms, the development of fish larvae needs to be synchronized in such a way that yolk reserves are exhausted as copepod larvae become available at peak abundance.

During the first few weeks after hatching, larvae do not migrate far away from the spawning area, but remain over the shelves (Efremenko, 1983). Larvae which develop into fingerlings may disperse later over the ocean and away from the continental shelves. This dispersal has been recorded in species such as Notothenia neglecta (White et al., 1982) and N. rossii marmorata (Burchett, 1983a) in the Scotia Sea, where young fish may be carried by the currents into lower latitudes from the South

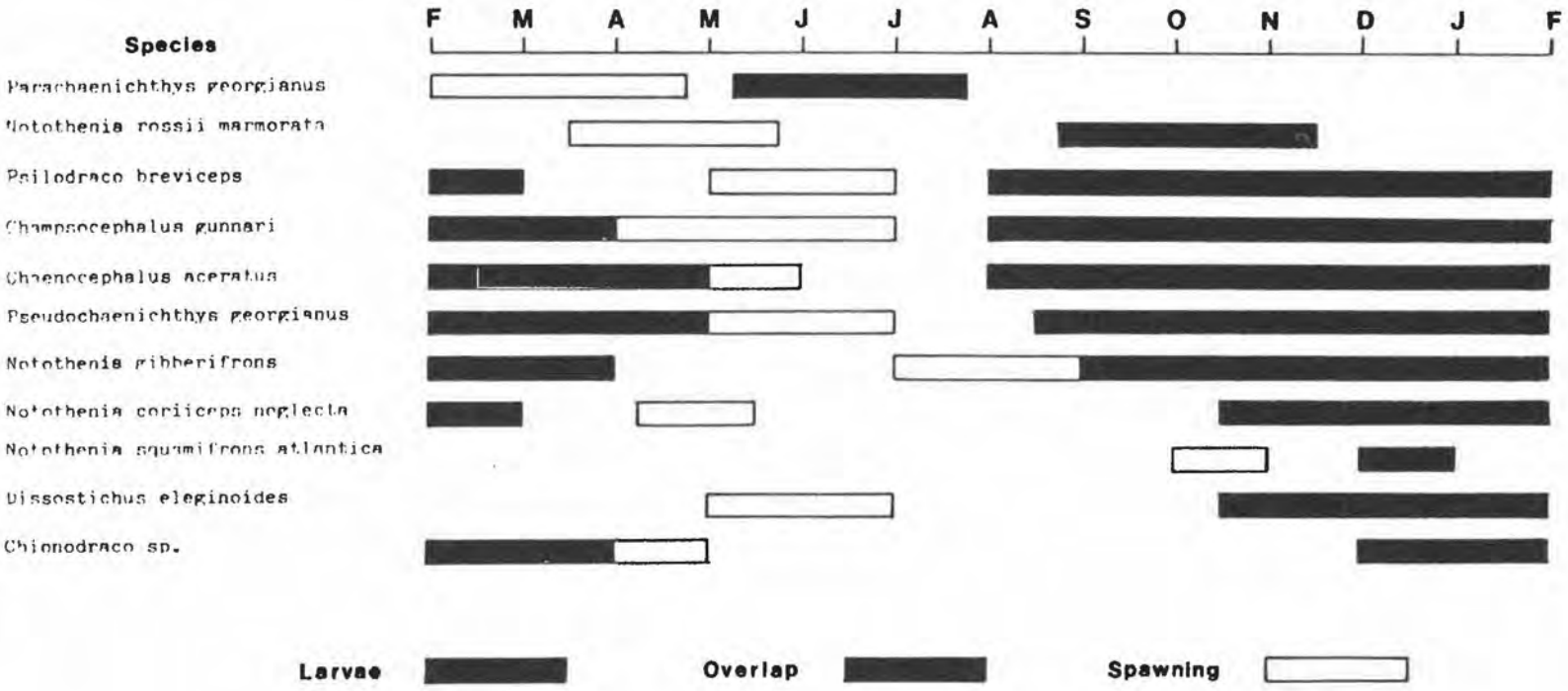
Table 16. Spawning data for Antarctic fish. See Table 15 for references.

SPECIES OF FISH	SPAWNING AREA	SPAWNING PERIOD	REF
Micromesistius australis	Patagonia	Spring	1
Merluccius hubbsi	Patagonia	December	2
Muraenolepis microps	South Georgia	Winter ?	3
Notothenia gibberifrons	South Georgia	Jul. - Aug.	4
N. gibberfrons	Atlantic sector		5
Notothenia coriiceps neglecta	South Orkneys	May	6
N. c. neglecta	Scotia Sea		4
N. c. neglecta	Terre Adelie		7
N. c. neglecta	South Georgia	Apr. - May	8
N. rossii rossii	Kerguelen	June	9
Notothenia rossii marmorata	South Georgia	Apr. - May	4
N. rossii marmorata	South Georgia	April	10
N. rossii marmorata	Atlantic sector		5
Notothenia magellanica	Kerguelen	Feb. - Mar.	7
Notothenia cyanobrancha	Kerguelen	Jan. - May	7
Notothenia kempi	South Orkneys		4
N. kempi	Atlantic sector		5
Notothenia larseni	South Orkneys		4
N. larseni	South Georgia		4
N. larseni	Atlantic sector		5
Notothenia nudifrons	Scotia Sea		4
N. nudifrons	South Shetlands		4
N. nudifrons	Atlantic sector		5
Notothenia augustifrons	South Sandwiches		4
Notothenia squamifrons	Atlantic sector		5
N. squamifrons	Kerguelen	October	9
Trematomus hansoni	Terre Adelie		7
T. hansoni	Atlantic sector		5
Trematomus bernacchii	East Antarctica	October	7
T. bernacchii	Davis Sea (66°S)	Oct. - Nov.	12
Trematomus vicarius	South Georgia	May	8
Pagothenia borchgrevinki	Davis Sea (66°S)	Jun. - Jul.	12
Dissostichus eleginoides	Kerguelen	June	14,15
D. mawsoni	----	Nov. - Dec.	17
Pseudochaenichthys georgianus	South Georgia		16
P. georgianus	South Georgia	April	8
Psilodraco breviceps	Scotia Sea	Autumn	3
Champsocephalus gunnari	South Georgia	May - Jun.	10
C. gunnari	South Georgia	April	18,19
C. gunnari	S. Shets./Elephant I.		18
C. gunnari	South Georgia	Mar. - May	20
C. gunnari	Kerguelen	Mar. - May	20
C. gunnari	Kerguelen	April	9
C. gunnari	South Georgia	April	22
C. gunnari	South Georgia		3
C. gunnari	South Orkneys		3
Chaenocephalus aceratus	South Georgia		3
C. aceratus	South Orkneys		3
C. aceratus	South Georgia		18
C. aceratus	South Orkneys		18
C. aceratus	Elephant Island		18
C. aceratus	South Georgia	Apr. - May	21
Channichthys rhinoceratus	----	Feb. - Mar.	23
C. rhinoceratus	Kerguelen	Feb. - Mar.	9
Pseudochaenichthys georgianus	South Georgia	Mar. - Apr.	3
Ps. georgianus	South Georgia	Apr. - Jun.	11
Chionodraco sp.	Scotia Sea	Mar. - Apr.	3

Table 17. Spawning season and spawning locations for selected species of Antarctic fish. (From Chojnacki and Palczewski, 1981).

ANTARCTIC SPRING		ANTARCTIC SUMMER				ANTARCTIC AUTUMN		ANTARCTIC WINTER			
(SPRING) Nov. - Dec.		(SUMMER) Jan. - Feb.		(LATE SUMMER) Mar. - Apr.		(AUTUMN) May - Jun.		(EARLY WINTER) Jul.-Aug.		(LATE WINTER) Sep.-Oct.	
SPECIES	LOCATION	SPECIES	LOCATION	SPECIES	LOCATION	SPECIES	LOCATION	SPECIES	LOCATION	SPECIES	LOCATION
M. australis	Patag.	N. magellanica	Kerg.	N. coriiceps n.	S.G.	N. coriiceps n.	S.O.	M. microps	S.G.	M. microps	S.G.
T. bernacchii	Davis	N. cyanobrancha	Kerg.	N. rossii m.	S.G.	N. coriiceps n.	S.G.	N. gibberifrons	S.G.	N. squamifrons	Kerg.
T. hansoni	---	N. coriiceps n.	T.Ad.	N. magellanica	Kerg.	N. rossii r.	Kerg.	P. borchgrevinki	Davis	T. bernacchii	T. Ad.
D. mawsoni	---	C. rhinocerataus	Kerg.	P. georgianus	S.G.	N. rossii m.	S.G.				
				C. gunnari	S.G.	N. nudifrons	Scot.				
				C. gunnari	Kerg.	N. larseni	Scot.				
				C. aceratus	S.G.	N. kempi	Scot.				
				C. rhinoceratus	Kerg	T. vicarius	S.G.				
				Ps. georgianus	S.G.	P. borchrevinki	S.G.				
				Chinodraco sp.	Scot.	D. eleginoides	Kerg.				
						P. breviceps	Scot.				
						C. gunnari	S.G.				
						C. gunnari	Kerg.				
						C. aceratus	S.G.				
						Ps. georgianus	S.G.				

Fig.15 . Spawning period and presence of early larvae for selected species of Antarctic fish from the Scotia Sea and Scotia Arc Islands.



Orkneys and the South Shetland Islands to South Georgia and the South Sandwich Islands.

In summary, it is likely that spawning dates occur in such a manner as to produce fish larvae in time for the primary production and subsequent zooplankton blooms of summer. Slight differences in spawning, hatching, and spawn-hatch times, coupled with advanced levels of development at hatching, provides flexibility that enhances survival of the young in response to annual variations in the environment and availability of zooplanktonic food.

Food Habits

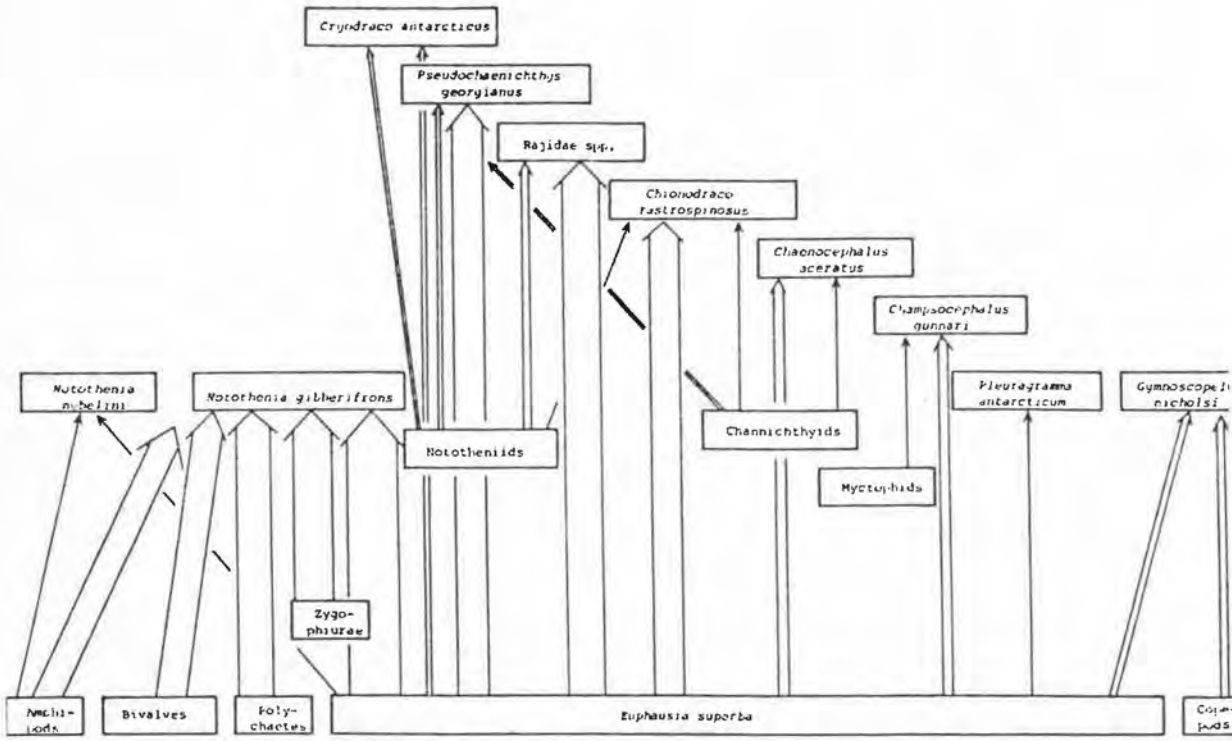
Knowledge of the feeding ecology of Antarctic fish is becoming increasingly important in light of increased human impact on fish stocks and their food supplies. Information on feeding ecology is crucial for an understanding of the trophic role played by Antarctic fish (Fig. 16). In recent years a large volume of literature dealing with Antarctic fish feeding ecology has been published. It relates mostly to the Nototheniiform fish, especially the two major families, Nototheniidae and Channichthyidae. The diet and behavior of the deep water groups such as the Myctophidae are less studied. Noteable studies on the feeding ecology of fish in Antarctic waters have been undertaken by Hureau (1970), Permitin (1970), Yukhov (1971), Permitin and Tarverdiyeva (1972, 1978), Tarverdiyeva (1972), Richardson (1975), DeWitt and Hopkins (1977), Moreno and Osorio (1977), Hoshiai (1979), Kompowski (1980a, 1980b), Moreno and Zamorano (1980), Tarverdiyeva and Pinskaya (1980), Duhamel (1981), Kock (1981, 1984), Targett (1981), Wyanski and Targett (1981), Daniels (1982), Burchett (1982, 1983c), Takahashi (1983), and Duhamel and Hureau (1984).

The availability of food depends to a large degree on the habitat occupied by the fish. Fish can be grouped into demersal (bottom living), demerso-pelagic (above the bottom), and pelagic (free swimming) species. Pelagic fish may inhabit the first 200m of surface waters (epipelagic) or deeper waters between 200-1000m (mesopelagic). In addition, they can be found over continental shelf areas (neritic province) or in deep waters beyond the continental edge (oceanic province). Equivalent, demersal, and demerso-pelagic fish may be encountered in sublittoral shallows (0-50m) or bathydemersally (1000m+). Table 18 lists the common Antarctic fish species in these categories according to morphological, dietary, and capture information.

Pelagic food availability

Major taxa in the Southern Ocean in terms of biomass are probably copepods, euphausiids, salps, and fish larvae, with cnidarians and pteropods important locally (Everson, 1984b). Zooplankton available to fish include grazers (herbivores) and predators (carnivores). Grazers frequently found in fish stomachs include the calanoid copepods, small euphausiids, medusae, ctenophores, and salps, while examples of

Fig. 16. The food chain of the demersal fish community to the north of the South Shetland Islands. (From Takahashi, 1983).



carnivorous zooplankton include the large euphausiids, euchaeted copepods, chaetognaths, amphipods, and pteropods (Everson, 1984a). Herbivores usually are more important prey items, both in numbers and biomass (Hopkins, 1971).

Because Antarctic fish spawn large, yolky eggs mostly during late summer and autumn, embryonic development over winter allows larval fish to hatch at an advanced stage coinciding with phytoplankton blooms and abundant zooplankton grazers (especially copepods). The abundance of summer zooplankton is reflected in increased summer growth rates for juvenile and adult fish, and in turn is linked to the rapid build up of fish reproductive tissue in late summer.

In general, many zooplanktonic prey spend summer months near or at the surface of the epipelagic zone (1-200m) and the winter period (May to August) deeper in the water column or under the ice (David, 1955, 1958, 1965; Hopkins, 1971). Staying near the surface during summer allows herbivores to graze on seasonal bursts of primary production and allows carnivores to prey on the herbivores. Both demersal and pelagic fish benefit from the vertical migration and swarming behavior of invertebrate zooplankton. In winter, deeper dispersal of zooplankton may bring them near the seabed in shallow water areas such as the continental shelves and sublittoral zone surrounding the Antarctic Continent and many Antarctic islands. This change in distribution allows demersal and demerso-pelagic fish to prey on zooplankton which is normally unavailable (Kompowski, 1980a; Naito and Iwami, 1982).

In summer, zooplankton near the surface increase in abundance primarily due to seasonal vertical migration (Foxton, 1956) and to a lesser extent from reproductive and growth cycles. Many pelagic fish, especially at their larval and juvenile stages, feed on concentrated zooplankton at this time. For example, juvenile Champsocephalus gunnari is often a by-catch species in krill swarms (Kompowski, 1980b). Similarly, krill, salps, gammarids, and hyperiids are often found in the stomachs of demersal and demerso-pelagic fish such as Notothenia kempi, N. gibberifrons, N. rossii, Chaenocephalus aceratus, and Chionodraco species (Tarverdiyeva and Pinskaya, 1980). When epipelagic concentrations of summer zooplankton (especially in the top 50m) sometimes extend into the nearshore sublittoral zone, these zooplankton become available to demersal fish species present in that zone. Pelagic zooplankton have been identified in the stomach contents of Notothenia rossii juveniles nearshore at South Georgia (Hoshiai, 1979) and krill have been confirmed in the diet of N. gibberifrons from the shallows at the South Shetland Islands (Takahashi, 1983).

Demersal food availability

Demersal fish, as well as some demerso-pelagic species, appear to rely on benthic prey as a major food source (Targett, 1981; Burchett et al., 1983). Variations in the assemblage of invertebrate benthos differs with depth, location, and to a lesser extent with season (Daniels, 1982) and is reflected in fish diet. Much of the benthic infauna is

Table 18. Ecotypes of selected species of Antarctic fish based upon body morphology, diet and depth of capture.

Demersal Fish Species	Zone	Demerso-pelagic Fish Species	Zone	Pelagic Fish Species	Zone
Raja georgiana	3	Notothenia larseni	2,3	Pleuragramma antarcticum	5,6
R. murrayi	2	N. rossii marmorata (adult)	2,3	Dissostichus mawsoni	5,6
R. eatonii	2	N. rossii rossii	2,3	D. eleginoides	3
Notothenia gibberifrons	2,3	N. magellanica	2,3	Micromesistius australis	3
N. nudifrons	1,2,3	Trematomus hansoni	2,3	Electrona antarctica	6
N. rossii marmorata (juv.)	2	T. newnesi	2,3	Gymnoscopelus nicholsi	6
N. rossii rossii (juv.)	2	Champsocephalus species	2,3	Notolepis coatsi	6
N. coriiceps neglecta	2	Chaenocephalus aceratus	2,3	Larvae and post-larvae of	5
N. angustifrons	1,2	Pseudochaenichthys georgianus	2,3	many fish species and young	
N. kempi	2,3		2,3	of Champsocephalus gunnari	
N. cyanobrancha	2			and Myctophidae.	
N. squamifrons	2,3				
N. magellanica	1,2				
Trematomus species	2,3				
Harpagifer species	1,2				
Artedidraco species	2,3				
Pogonophryne species	3,4				
Muraenolepis microps	2,3				
Psilodraco breviceps	2				
Pseudochaenichthys species	2				
Channichthys rhinoceratus	2				
Chionodraco species	2,3				

KEY

ZONE	ECOTYPE	DEPTH
1	Littoral	0 - 3 meters
2	Sublittoral	3 - 200
3	Archidemersal	200 - 1000
4	Abyssoldemersal	1000+
5	Epipelagic	0 - 200
6	Mesopelagic	200 - 1000

unavailable to fish with the possible exception of Notothenia gibberifrons (Moreno and Osorio, 1977). The epifaunal invertebrates are important prey items for most bottom living fish and are available all year round (Burchett, 1983c).

Feeding behavior

Demersal and demerso-pelagic fish show great diversity in feeding behavior and the type of prey consumed (Targett, 1981; Daniels, 1982). Diversity in diet and feeding behavior appear greatest among the demersal and demerso-pelagic Nototheniids, especially in nearshore fish communities less than 90 m deep (Burchett, 1982; Burchett et al., 1983). Demersal Nototheniids prey primarily on amphipods, isopods, fish (mostly larvae, postlarvae, and young fish), polychaetes, decapods, gastropods, and bivalves (Targett, 1981; Daniels, 1982). Dietary examination of Channichthyids by Permitin and Tarverdiyeva (1972, 1978) and Daniels (1982) demonstrated that these fish are indeed specialized feeders. Most Channichthyids are planktivorous feeders, with the exception of Chaenocephalus aceratus and Channichthys rhinoceratus, which consume a high proportion of fish (Hureau, 1970; Williams, 1983).

The most extensive studies of Antarctic fish feeding behavior have been undertaken in the nearshore water areas of approximately 0-5m in depth. Around certain sub-Antarctic and Antarctic Islands such as South Georgia and Kerguelen, the shallow, nearshore areas of 0-30m are often dominated by the macroalgae Macrocystis pyrifera, Himantothallus grandifolius, and Durvillea antarctica (Burchett, 1982; Duhamel, 1982), which create a specialized habitat not only for fish but for many of their prey. Burchett (1983c) and Burchett et al. (1983), studying the nearshore fish communities at South Georgia, found that much of the benthos upon which the fish feed were nocturnally active. Net hauls and SCUBA diving observations indicated that the fish in that area were also only active at night. As night length varied seasonally, there was a corresponding change in fish feeding activity. Notothenia rossii and N. neglecta actively grazed macroalgae, which appears to be an important dietary component at certain times of the year (Burchett, 1983c; Burchett et al., 1983). Algal consumption has also been observed by Everson (1970a), Hureau (1970), and Daniels (1982) for equivalent subspecies at the South Orkney Islands, Kerguelen, and the Antarctic Peninsula.

As indicated in Table 19, diets for individuals of the same species varies between locations (Rowedder, 1979; Naito and Iwami, 1982). For example, for Notothenia gibberifrons, N. larseni, T. scotti and Harpagifer bispinis, the diets of individuals of similar size caught at the same time of year but at different localities have significant differences in prey taken and in the amount of food consumed (Daniels, 1982).

Differerence in the diets of fish of different sizes has been noted by many authors for species such as Pleuragramma antarcticum (DeWitt and Hopkins, 1977), Pogonophyrne sp. (Wyanski and Targett, 1981), Notothenia

Table 19. Diets for selected species of Antarctic fish (X = found in stomach contents; + = the dominant or very common food item within a particular examination). This table was compiled from information in: Olsen, 1954, 1955; Permitin, 1969; Hureau, 1970; DeWitt, 1971; Yukhov, 1971; Permitin and Tarverdiyeva, 1972; Everson, unpublished results; Tarverdiyeva, 1972; Keysner et al., 1974; Richardson, 1975; DeWitt and Hopkins, 1977; Moreno and Osorio, 1977; Hoshiai, 1979; Moreno and Zamorano, 1980; Targett, 1981; Daniels, 1982; Naito and Iwami, 1982; Burchett, 1983c; Burchett et al., 1983; Duhamel and Pletikosic, 1983; Takahashi, 1983; Williams, 1983.

FISH SPECIES	*Bala georgiana*	*Micromesistius australis*	*Notothenia gibberifrons*	*Notothenia rossii rossii* (juv.)	*Notothenia rossii rossii* (adult)	*Notothenia rossii marmorata* (juv.)	*Notothenia rossii marmorata* (adult)	*Notothenia magellanica*	*Notothenia kempi*	*Notothenia larseni*	*Notothenia nudifrons*	*Notothenia cyanobrancha*	*Notothenia coriiceps coriiceps*	*Notothenia coriiceps neglecta*	*Notothenia squamifrons*	*Notothenia angustifrons*	*Trematomus bernacchii*	*Trematomus hansoni*	*Trematomus vicarius*	*Trematomus newnesi*	*Dissostichus mawsoni*	*Dissostichus eleginoides*	*Pleuragramma antarcticum*	*Champsocephalus gunnari*	*Chaenocephalus aceratus*	*Pseudochaenichthys georgianus*	*Harpagifer bispinis*	*Nuraenolepis microps*
PREY GROUPS																											
Porifera / Foraminifera			+						X	X							X										
Coelenterata			X						X									X									
Anthozoa			X						X																		
Hydrozoa																		X									
Ctenophora / Cnideria	X		X		X	+			X	+			X	X	X									X			
Nemertinia			X			X				X			X				+		X								
Nematoda											X																
Priapulida			X						X					X													
Bryozoa			X										X														
Chaetognatha									X	X													X				
Annelida	X		+	X		X		X	+	+	+	X	+	+		+	+	X	X	X			X	X			
Polychaeta	X		+	X		X		X	+	+	+	X	+	+		+	+	X	X	X			X	X			
Crustacea (arthropoda)	+	+	+	+	X	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			X	+	+	+	X	+
Ostacoda			X			X					X		X		X		X										
Copepoda			X			X			X	+	X		X		X		X						+				
Malacostraca	+	+	+	+	X	+	+	+	+	+	+	+	+	+	+	+	+	+	+				X	+	+	+	X	+
Mysidacea	+		+			+	X		X	+	+		X			+							X	X	+	X		
Cumacea			X			X			X	X	X					X								+				
Isopoda	X		X	+		+		+	+	X	+	X	+	+	+	X	+	X	X				X					+
Euphausiacea	+	+	+	X	X	X	+	X	+	+	+		+	+	X	+	+	+	+				X	+	+	+		X
Amphipoda	X		+	+		+		+	+	+	+	+	+	+	+	+	+	+	+					+	X	X	X	+
Decapoda (shrimps, prawns)	+		X	X		X		+	X	X	X		X		X		X	X					X	X		+	X	X
Pycogonida			X								X						X											
Mollusca	X		+	X		X		+	+	X	X	+	+	+	X	X	+	+		+	X	X	X	X	X		+	+
Amphineura									+													X						
Gastropoda			+	X		X		X	X	X	X		+	+														
Opisthobrancha			X						X								X											
Bivalvia			+	X		X		+			X		X	X		X	X				X							
Scaphopoda			X										X															
Cephalopoda	X		+						+		X	+	X	+			+						X		X			
Echinodermata	X		+			X			+	X	X	X	X		X	X	X	X		+			X		X		+	+
Crinoidea			X						X		X															X		
Ophiuroidea			+						+	X					X											X		
Echinoidea			+						+							X										X		
Holothuriodea			X			X							X															
Salpidae (tunicates)			+		X	X	X		+	X	X			X	X		X											
Ascidiae			X			X			X																			
Fish	+		X	+		+	X	+	X	X	X		+	X	X	X	X	X	X		+	+	X	X	+	+		X
Notothenidae	X								X				X		X							+			X	X		
Channichthyidae																									X	X		
Other fish	X		X												X									X		X		
Fish larvae and fingerlings										X					X							+						
Eggs			X						X	X	X		X					+	+			+				X		
Algae	+		+	+		+		+	+	X			+	+			+	+		X					X		X	X
Diatoms									X				X															

gibberifrons, N. magellanica, and Champsocephalus gunnari (Takahashi, 1983), N. magellanica (Blankley, 1982), and Dissostichus eleginoides (Duhamel and Pletikosic, 1983). In all species studied, prey size, prey quantity consumed, and numbers of different prey types taken increased with fish size.

Seasonal changes in the diet of many demersal and demerso-pelagic fish have been demonstrated. Burchett (1983c) found that juvenile Notothenia rossii have a more varied diet in summer months. The relative frequency of consumption of major prey items varied throughout the year with definite seasonal variations in numbers of amphipods, polychaetes, and bivalves consumed. Differences in the diet of similar sized individuals of Notothenia gibberifrons, N. nudifrons, N. larseni, and Trematomus scotti collected at the same location at different times of year were significant in the relative importance of each prey taxon, but tended to show no significance in the amount of food consumed (Daniels, 1982). In all four species studied by Daniels (1982), individuals tended to consume prey from the same number of taxa. Spring samples normally contained prey of a smaller size than late summer samples.

In summary, demersal fish use a wide variety of behavioral and morphological mechanisms that reduce intraspecific and interspecific competition (Burchett, 1982). For generalist feeding species, these mechanisms include switching prey type and feeding strategies. Targett (1981) concluded that the low diversity of Antarctic prey species precluded the necessity for fine division of food resources vertically. Feeding niche differences, perhaps evolved by Nototheniids as an adaptation to avoid prey competition, may contribute to the success and dominance of demersal Nototheniids in these communities.

Role in the Ecosystem

Antarctic fish play an important part in the marine community. They are both important prey species for many predators, as well as major predators themselves on a variety of plankton. As commercial fisheries exploit fish stocks and their prey (e.g., krill), an increased understanding of fish ecology will allow better assessment of the impact of human activities on the marine ecosystem.

Importance to predators

Within the Antarctic marine ecosystem, it is estimated that about 2 million tons of fish are consumed annually by predators (Everson, 1977). Of this amount, 77% is taken by seals (47% by elephant seals and the rest by fur, crabeater and Weddell seals) and 18.5% is taken by birds (mostly white-chinned petrels (10%) and macaroni penguins (4%) (Croxall et al., 1984)). Studies in the Scotia Sea indicate that of all fish consumed, approximately 82% by weight are consumed by seals, 8% by cape pigeons, 3% by penguins, 2% by blue-eyed shags, and 2% by snow petrels (Croxall et al., 1984). It appears that Antarctic fur seals are taking fish primarily during winter, although the food habits for that period are poorly known (Doidge and Croxall, 1984).

Knowledge about fish in the diets of Antarctic birds is limited. The albatrosses are known to take Pseudochaenichthys georgianus (Channichthyidae) and various Notothenia species (Prince, 1980b). Fish of these families are also the main prey of the diving seabirds such as the shags and penguins. Diets of these seabirds vary between different Antarctic locations. By weight, Notothenia nudifrons comprises 75%, N. rossii 14%, and Trematomus newnesi 7% of the diet of blue-eyed shags at Signy Island, South Orkney Islands (Shaw, unpublished data). Notothenia rossii, N. larseni, and Champsocephalus gunnari are about of equal importance in the diet of the gentoo penguin at South Georgia (Croxall and Prince, 1980).

Weddell seals in the Scotia Sea take various Notothenia and Trematomus species, but elsewhere often prey on Dissostichus species (Øritsland, 1977). Percentage weight of fish in the diet of the Antarctic fur seal in summer at South Georgia consists mostly of Champsocephalus gunnari (76%), Notothenia rossii (5%), and a variety of other Notothenia species (8%) (North et al., 1983). Antarctic fur seals take a relatively wide range of fish, including the semi-pelagic Champsocephalus gunnari rather than Nototheniid species, and consume mostly young adults of 3 - 5 years old (North et al., 1983). The diet of Commerson's dophins near the Kerguelen Islands consists mainly of Champsocephalus gunnari (Robineau and Duhamel, 1984).

Importance of krill and possible effects of exploitation

The importance of krill in the diet of many fish varies greatly according to water depth, habitat, locality, season, fish size, and behavior. Krill is the single most important food item for adult pelagic fish (Permitin and Tarverdiyeva, 1972; DeWitt and Hopkins, 1977) as well as the pelagic young and juvenile stages of species such as Champsocephalus gunnari (Kompowski, 1980a). The dietary importance of krill for demersal and demerso-pelagic fish also varies (Permitin and Tarverdiyeva, 1972). Tarverdiyeva and Pinskaya (1980) noted that both the absolute and relative number of plankton-feeding fish that prey upon krill diminishes from higher to lower Antarctic latitudes. Thus, near the Antarctic Peninsula krill often constitutes 100% of fish diets, off the South Shetland Islands 80%, off the South Orkney Islands 67%, and at South Georgia 30% (Permitin and Tarverdiyeva, 1972; Takahashi, 1983).

Because of the importance of krill in the diet of both demersal and pelagic fish, heavy harvesting of krill resources may affect fish populations. Potential effects are likely to be greatest on species such as Pleuragramma antarcticum, Notothenia rossii, and Champsocephalus gunnari which take large amounts of krill at certain stages in their life cycles. The latter two species are also the two most commercially valuable fish species. Heavy fishing of krill will probably have less effect on the majority of the demersal fish species because they have alternative benthic food supplies.

CHAPTER 6: ANTARCTIC SEABIRDS

Introduction

Seabirds are an important component of the Antarctic marine ecosystem. Of the many seabirds present in Antarctica, perhaps the most specialized are the penguins, which dominate the avifauna biomass. These flightless predators are uniquely suited to marine life in higher latitudes. There is a large body of literature dealing with Antarctic seabirds and a comprehensive review is beyond the scope of this paper. Several papers have outlined previous work (Murphy, 1936; Murphy, 1964; Voous, 1965; Carrick and Ingham, 1967, 1970; Stonehouse, 1967, 1975; Prevost and Mougin, 1970; Watson et al., 1971; Watson, 1975; Mougin, 1975). The review by Croxall (1984) provides a recent summary and synthesis of Antarctic seabird ecology and biology.

Species Composition and Abundance

Table 20 lists the seabirds found in Antarctic waters. Although not all of these species breed south of the Antarctic Convergence, most are present south of the convergence during at least part of the year. The Procellariiformes, including the albatrosses, petrels, shearwaters, and prions is the group with the most Antarctic species. But, in terms of abundance, the Sphenisciformes, or penguins, are clearly the most important (Croxall, 1984).

Several investigators have attempted the difficult task of estimating the abundance of penguin and other seabirds (Croxall and Kirkwood, 1979; Croxall and Prince, 1979, 1980a; Williams et al., 1979; Mougin and Prevost, 1980; Prevost, 1981; Ainley et al., 1984; Croxall, 1984). These estimates reveal the prominence of penguins in Antarctic avifauna (Table 21). Although penguins are clearly a major portion of the Antarctic avifauna, Ainley et al. (1984) pointed out that penguins may not account for as high a proportion (80% - 90%) of total Antarctic bird biomass as has been estimated in the past. They suggested that the population size of other seabirds may have been underestimated because these are less accessible and difficult to census.

Distribution

The distribution of the flighted seabirds was reviewed by Murphy (1964), Falla (1964), Voous (1965), Carrick and Ingham (1967, 1970), and Watson (1975). Most species occur in a circumpolar zone which fluctuates seasonally in response to the advancing and retreating ice-edge (Mackintosh, 1960). Oceanic fronts are also important features in determining the distribution of seabirds (Ainley and Boekelheide, 1983). Ainley et al. (1984) noted, for example, that the Antarctic Slope Front is a major biological/physical interface which attracts large groups of foraging seabirds. The distribution of penguins and other seabirds as summarized by Croxall (1984) is presented in Table 22. The breeding

Table 20. Antarctic seabirds. (Data from Watson, 1975; Bengtson, 1978; Croxall, 1984).

GROUP	SPECIFIC NAME	COMMON NAME
SPHENISCIFORMES	Aptenodytes forsteri	emperor penguin
	A. patagonicus	king penguin
	Pygoscelis adeliae	adelie penguin
	P. antarctica	chinstrap penguin
	P. papua	gentoo penguin
	Eudyptes chrysocome	rockhopper penguin
	E. chrysolophus	macaroni penguin
	Spheniscus magellanicus	magellanic penguin
PROCELLARIIFORMES	Diomedea exulans	wandering albatross
	D. epomophora	royal albatross
	D. melanophris	black-browed albatross
	D. chrysostoma	grey-headed albatross
	D. cauta	shy albatross
	Phoebetria fusca	sooty albatross
	P. palpebrata	light-mantled sooty albatross
	Macronectes giganteus	southern giant petrel
	M. halli	northern giant petrel
	Fulmarus glacialoides	Antarctic fulmar
	F. glacialis	northerm fulmar
	Pagodroma nivea	snow petrel
	Thalassoica antarctica	Antarctic petrel
	Daption capense	cape pigeon
	Pachyptila belcheri	narrow-billed prion
	P. desolata	dove prion
	Halobaena caerulea	blue petrel
	P. lessonii	white-headed petrel
	P. brevirostris	Kerguelen petrel
	P. inexpectata	mottled petrel
	P. mollis	soft-plumaged petrel
	Pterodroma incerta	Atlantic petrel
	Procellaris aequinoctialis	white-chinned petrel
	P. cinerea	grey petrel
	Puffinus griseus	sooty shearwater
	P. tennuirostris	short-tailed shearwater
	Oceanites oceanicus	Wilson's storm petrel
	Fregetta tropica	black-bellied storm petrel
	Pelecanoides georgicus	South Georgia diving petrel
	P. urinatrix	common diving petrel
PELECANIFORMES	Phalacrocopax albiventer	king shag
CHARADRIIFORMES	Catharacta maccormicki	south polar skua
	C. lonnbergi	brown skua
	Larus dominicanus	southern black bucked gull
	Sterna vittata	Antarctic tern
	S. paradisaea	Arctic tern
	S. virgata	Kerguelen tern

Table 21. Biomass and energy consumption of Antarctic seabirds. (After Croxall, 1984).

	Sub-Antarctic		Antarctic		Total	
	Biomass (tons x 10^6)	Energy Consumption (kcal x 10^{12} y^{-1})	Biomass (tons x 10^6)	Energy Consumption (kcal x 10^{12} y^{-1})	Biomass (tons x 10^6)	Energy Consumption (kcal x 10^{12} y^{-1})
Penguins	410	22.3	198	14.1	608	36.4
Other Species	53	5.1	3	0.5	56	5.6
Total	463	27.4	201	14.6	664	42.0

distribution of Antarctic penguins varies by species from north to south (Fig. 17). For example, of the three Pygoscelid species, adelie penguins breed farthest south, chinstrap penguins at somewhat lower latitudes, and gentoo penguins closest to the Antarctic Convergence (Sladen, 1964; Watson et al., 1971). These species are by no means mutually exclusive and in a few places, such as at King George Island in the South Shetland Islands, all three species are sympatric (Trivelpiece and Volkman, 1979).

Carrick and Ingham (1967) suggested that the distribution of penguins was closely tied to suitable breeding and feeding habitat. Pygoscelid species require ice-free rookery areas near predictable local food sources. In contrast, ice-breeding species such as the Emperor penguin must have predictable and stable fast ice in areas accessible to good feeding grounds. The expanding distribution of certain penguin species during recent decades (Croxall and Kirkwood, 1979) may have resulted from increased availability of food within foraging range of suitable breeding habitat (Sladen, 1964; Conroy, 1975).

Movements

Antarctic seabirds are known to move considerable distances in response to prey availability and physical factors such as ice (Falla, 1964; Voous, 1965; Carrick and Ingham, 1970; Ashmole, 1971; Watson, 1975). Watson et al. (1971) noted that seasonal migrations of sooty shearwaters, gadfly petrels, prions, blue petrels and several other albatrosses are probably in response to abundant food supplies at higher latitudes in summer.

The winter movements and distribution of birds in Antarctica are less certain. Most penguins are thought to remain south of the Antarctic Convergence, but flighted birds may move further north (Oordt and Kruyt, 1953; Tickell, 1967; Parmelee, 1976; Prince, 1980b). Adelie and chinstrap penguins are thought to remain in the pack ice zone during the winter, and may swim or be carried by ice long distances from their breeding areas (Routh, 1949; Szijj, 1967).

Despite the long-range movements carried out by flighted seabirds and that potentially may be undertaken by penguins, exchange between populations may be limited. The high degree of nest site and birth site fidelity in seabirds probably reduces genetic interchange between different breeding groups. For example, Watson et al. (1971) noted the striking difference in the sizes between northern and southern colonies of gentoo penguins. They interpreted these morphometric difference as evidence of limited gene flow between the two groups.

Reproduction

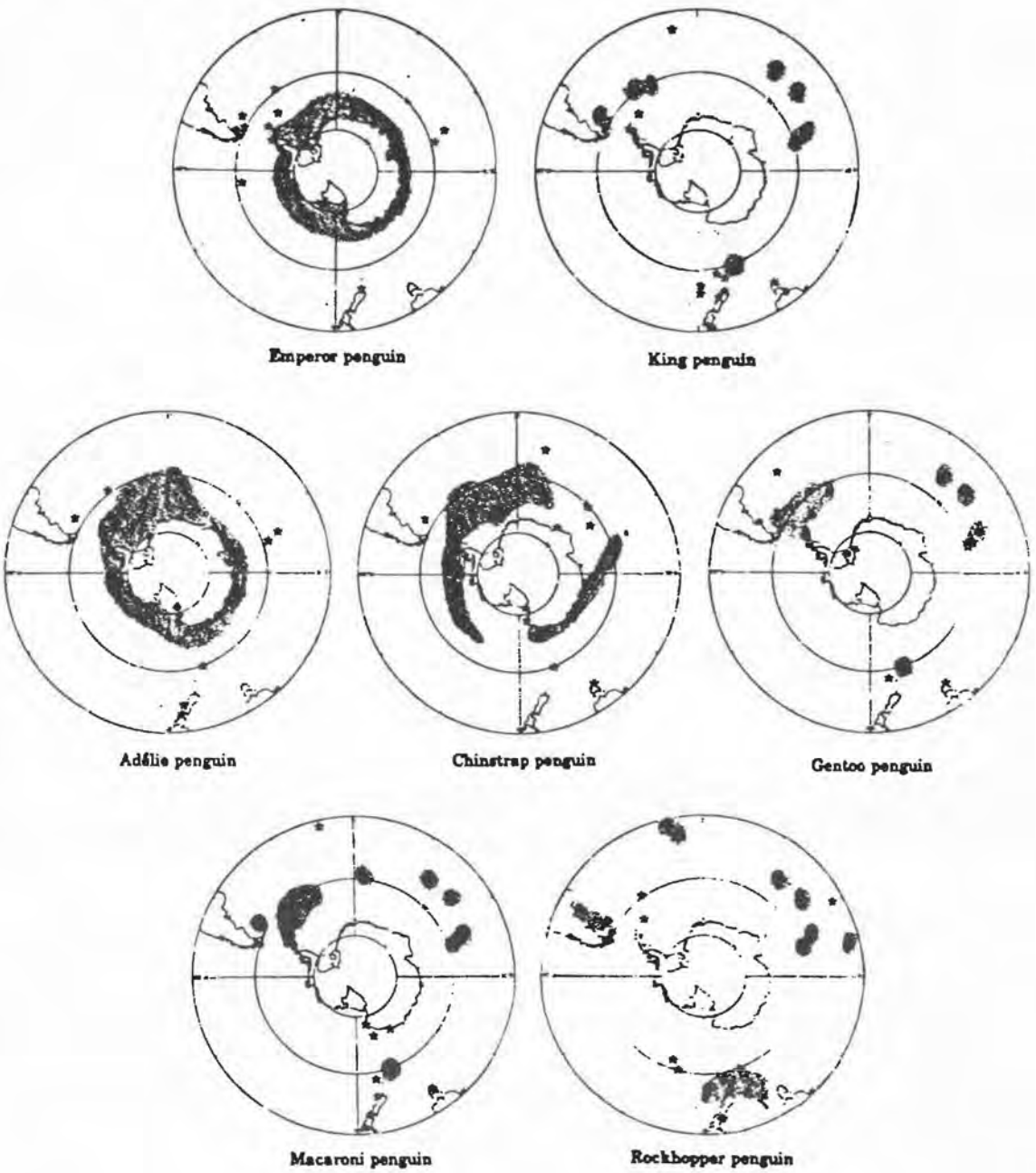
Reproductive biology and behavior has been investigated for many Antarctic seabirds including: penguins (Taylor, 1962; Tenaza, 1971; Trivelpiece and Volkman, 1979; Volkman and Trivelpiece, 1980; Ainley et al., 1983), skuas (Jones and Skira, 1979; Jouventin and Guillotin, 1979;

Table 22. Breeding distributions of Antarctic, subAntarctic, and selected southern hemisphere seabirds. (From Croxall, 1984).

	Amsterdam I.	St. Paul I.	Tristan da Cunha	Gough I.	Marion I.	Prince Edward I.	Crozet I.	Kerguelen I.	Macquarie I.	Heard I.	South Georgia	Antipodes I.	Auckland I.	Campbell I.	Falkland I.	South Shetland I.	South Orkney I.	South Sandwich I.	Antarctic Peninsula	Bouvet I.	Antarctic Continent
PHENISCIFORMES																					
Aptenodytes forsteri*																			+		+
Aptenodytes patagonicus*						+	+	+	+	+	+				+						
Pygoscelis adeliae*																+			+	+	+
Pygoscelis papua*						+	+	+	+	+	+				+	+			+		
Pygoscelis antarctica*											+					+			+	+	+
Eudyptes chrysocome*	+[a]		+[a]		+	+	+	+	+	+	+	+	+	+	+	(+)					
Eudyptes chrysolophus[b]*					+	+	+	+	+		+				+	+			(+)	+	
Eudyptes sclateri												+	+	+							
Megadyptes antipodes													+	+							
Spheniscus magellanicus															+						
ROCELLARIIFORMES																					
Diomedea exulans*	+[c]		+		+		+	+			+	+	+	+							
Diomedea epomophora													+	+							
Diomedea melanophrys*							+	+	+	+	+	+		+	+						
Diomedea chrysostoma*					+		+	+			+			+							
Diomedea chlororhynchos*	+		+		+		+														
Diomedea cauta													+								
Phoebetria fusca*	+		+		+		+	+													
Phoebetria palpebrata*					+		+	+	+	+	+	+	+	+							
Macronectes giganteus*			+		+		+	+	+	+	+				+	+			+	+	+
Macronectes halli*			+		+		+	+			+	+	+	+							
Thalassoica antarctica*																					+
Daption capense*							+	+	+	+	+	+	+	+		+			+	+	+
Fulmarus glacialoides*																+			+	+	+
Pagodroma nivea*											+					+			+	+	+
Pachyptila belcheri*							+	+							+						
Pachyptila desolata*							+	+	+	+	+		+			+					(+)
Pachyptila vittata	+		+																		
Pachyptila salvini*					+		+														
Pachyptila crassirostris*										+			+								
Pachyptila turtur*					+		+		+		+	+			+						
Halobaena caerulea*					+		+	+	+		+										
Pterodroma macroptera*	(+)		+		+		+	+													
Pterodroma lessoni*							+	+	+			+	+								
Pterodroma brevirostris*			+		+		+	+													
Pterodroma mollis*	(+)		+		+		+	?				+									
Pterodroma incerta			+																		
Procellaria aequinoctialis*	(+)		+		+		+	+			+	+	+	(+)	+						
Procellaria cinerea*	(+)		+		+		+	+	(+)			+		(+)							
Puffinus griseus									+			+	+	+	+						
Puffinus carneipes	+																				
Puffinus gravis			+																		
Puffinus assimilis	+		+									+									
Oceanites oceanicus*	?						+	+		+	+				+	+			+	+	+
Fregetta tropica*					+		+	+			+	+	+			+				+	
Fregatta grallaria	+		+																		
Garrodia nereis*			+		+		+	+	?		+	+	+	(+)	+						
Pelagodroma marina	(+)		+										+								
Pelecanoides georgicus*					+		+	+		+	+		+								
Pelecanoides urinatrix*	(+)		+		+		+	+	+	+	+	+	+		+						
PELECANIFORMES																					
Phalacrocorax albiventer[d]*					+		+	+	+						+						
Phalacrocorax atriceps*										+	+					+			+		
Phalacrocorax magellanicus															+						
Phalacrocorax campbelli													+	+							
Phalacrocorax melanoleucos														+							
CHARADRIIFORMES																					
Catharacta maccormicki*																+			+		+
Catharacta lonnbergi*	+		+		+		+	+	+	+	+	+	+	+	+	+			+	+	
Larus dominicanus*					+		+	+	+	+	+	+	+	+	+	+			+	?	
Larus maculipennis															+						
Larus novae-hollandiae													+	+							
Larus scoresbii															+						
Sterna fuscata	+																				
Sterna vittata*	+		+				+	+	+	+	+	+	+	+		+			+	+	
Sterna virgata*					+		+	+													
Sterna hirundinacea															+						
Anous stolidus			+																		
TOTAL	11		21		26		34	30	21	17	26	20	24	18	22	16			14	11	10

[a]Sometimes separated as E. moseleyi, [b]Includes E. schlegeli, [c]Describes as D. amsterdamensis (Roux et al., 1983), [d]Includes P. verrucosus, (+) probable or former breeding species, *species of chief interest (see p. 538).

Fig. 17. Distribution maps of the seven Antarctic penguin species known to breed south of the Antarctic Convergence. (From Watson, 1975).



Moors, 1980; Williams, 1980a, 1980b; Trivelpiece and Volkman, 1982), Kelp gulls (Fraser, in prep.), and Antarctic terns (Parmelee and Maxon, 1975; Parmelee, 1977).

The most comprehensive study to date of penguin breeding biology is the work of Ainley et al. (1983) who studied adelie penguins at Cape Crozier, Ross Island. After arrival at the rookery in spring, pairs court, and the female lays a clutch usually of two eggs Males generally incubate the egg for the first two or three weeks until relieved by the female. Males then depart to sea to feed. During the approximate five week incubation period, males and females alternate incubation shifts, which become shorter as hatching nears. After a brooding period of approximately 20 days, chicks move together into creches while waiting for their parents to return from the sea to feed them. At approximately 50 days of age, chicks are fledged and depart to sea.

Croxall (1984) noted that many procellariiformes have a reproductive pattern generally similar to penguins. Breeding birds arrive at the colony and undergo pair formation, nest building, and copulation. Prior to egg-laying, females may depart to sea to replenish energy reserves while the male stays ashore defending the empty nest site. The female lays a clutch when she returns and both mates alternately incubate until hatching. At that time both parents continue to make feeding trips to the sea to obtain food for their growing chick.

The timing of nesting seasons varies with latitude, life history of the species, and the seasonality of locally available food. Many species' reproductive season corresponds with the summer increase in zooplankton abundance (Fig. 18). The specific order and duration of reproductive activities for selected species was summarized by Croxall (1984) (Fig. 19).

Factors affecting breeding success vary annually and among species. For example, Berruti (1979) and Croxall and Prince (1979) noted that albatrosses and giant petrels generally have greater breeding success than penguins. There is also evidence that breeding success in penguins increases as birds gain more experience (Sladen et al., 1968; Ainley and Schlatter, 1972; Carrick, 1972; Ainley et al., 1983). Physical parameters, such as weather or ice, also affect breeding success in penguins. Yeates (1975) noted that poor weather conditions were often highly correlated with poor reproductive success in emperor and adelie penguins. Similarly, heavy ice conditions near rookeries can adversely affect breeding success (Stonehouse, 1963; Yeates, 1968; Ainley and LeResche, 1973; Croxall and Prince, 1979). Mild winter weather appears to promote increased breeding success in wandering albatrosses at South Georgia (Croxall, 1979). Hence, a variety of factors can affect breeding success at diverse sites from year to year. The cause and effect relationships between these variables requires further study.

Fig. 18. Timing of breeding seasons in Antarctic seabirds. Vertical bars represent hatching dates. Phytoplankton and zooplankton data from Hart (1942) and Foxton (1956) respectively. (From Croxall, 1984).

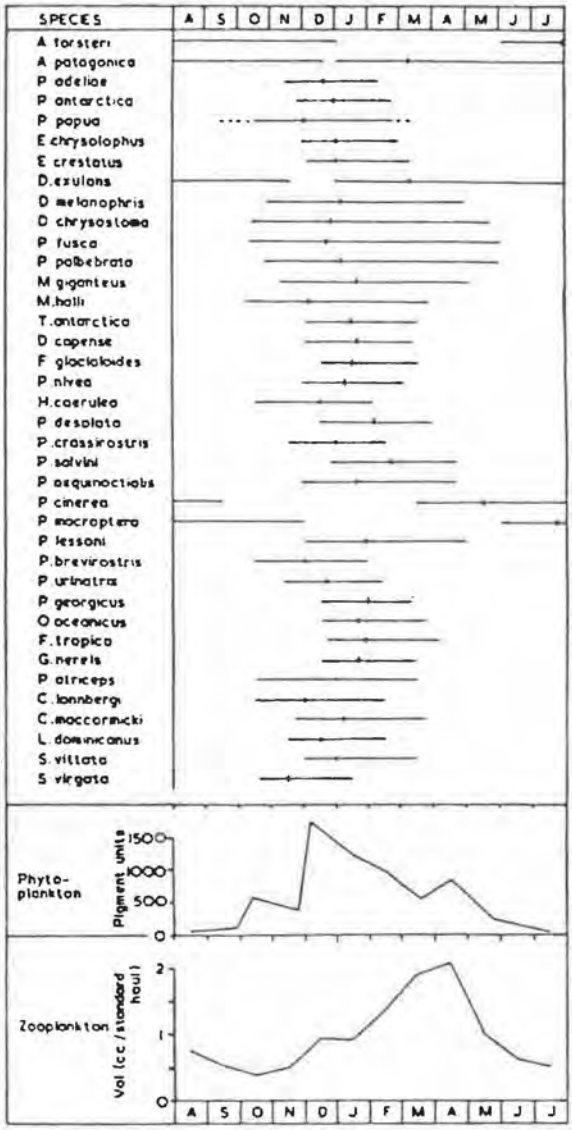
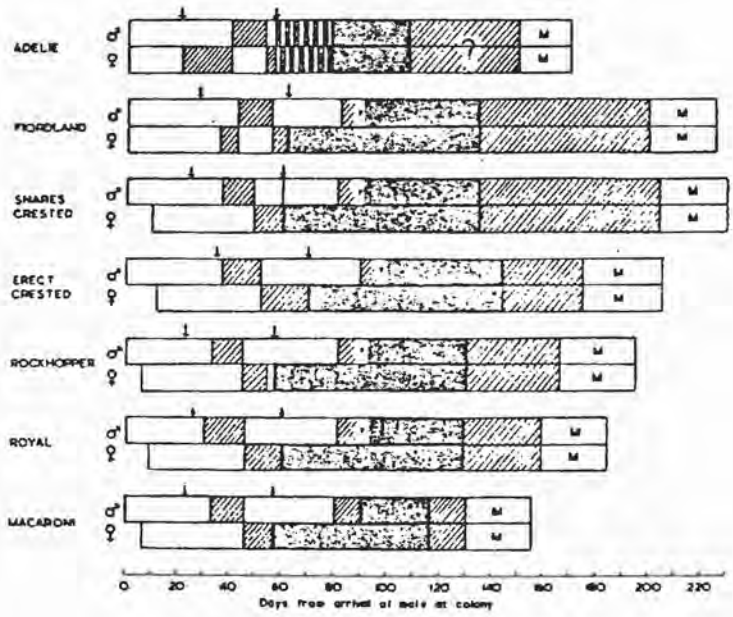


Fig. 19. Duration and timing of breeding season events in some Antarctic penguins. (Data from, in turn: Taylor, 1962; Spurr, 1975; Warham, 1974b, 1972b, 1963, 1971b; Croxall, unpublished). First arrow, mean laying date second egg; second arrow, mean hatching date; cross-hatched, at sea; strippled, feeding chicks; blank, in colony; M, moult. Periods of unknown duration indicated by ?. (From Croxall, 1984).



Food Habits

Prey

Ashmole and Ashmole (1967) and Croxall (1984) noted that the uncritical analysis of stomach contents can lead to misleading conclusions. Undigestible items, such as cephalopod beaks and fish otoliths, may accumulate and lead to an overestimation of the importance of these items. The summarized results from selected quantitative feeding studies are presented in Tables 23 and 24. Croxall (1984) noted that analyzing prey based on regurgitations and pellets avoids some of the problems outlined above. Still, the question of the dissolution rates of small fish otoliths must be considered. If otoliths are dissolved prior to regurgitation, the importance of such food items will be underestimated. Regurgitation and pellets were utilized by several authors (Imber, 1973; Berruti and Harcus, 1978; Berruti, 1979; Croxall and Prince, 1980a, 1980b, 1982; Clarke et al., 1981; Imber and Russ, 1975; Imber, 1976, 1981; Johnstone, 1977). Crustaceans are a principal prey of seabirds in general, with Euphausiids being the crustacean most frequently taken (Tables 23 and 24). This pattern is the case both for surface-feeding and diving birds. When krill are available at the surface, it is not uncommon for seabirds to form aggregations as they feed on these patches (Ozawa et al., 1968).

Different prey species are utilized by seabirds to varying degrees at different latitudes. For example, at higher latitudes, E. crystallorophias is a euphausiid most commonly eaten by seabirds (Laws, 1977b). At lower latitudes, copepods and amphipods are more important prey items (Harper, 1972; Imber, 1973, 1981; Strange, 1980; Prince, 1980a). These shifts in the relative importance of prey items correspond with the general pattern of zooplankton distribution and food webs suggested by Lubimova (1983). She suggested a krill-dominated food web in higher latitudes with increased dominance of copepods and amphipods in more northerly, ice free areas.

Sympatric species may partition food resources by feeding in different areas or by selecting prey of different sizes. For example, chinstrap and adelie penguins have been reported to take krill of different sizes at Signy Island (White and Conroy, 1975). Croxall and Prince (1983) found a size difference in the prey taken by gentoo and macaroni penguins at South Georgia. Similarly, Volkman et al. (1981) described differences in the size of krill taken by adelie and chinstrap penguins at King George Island. These differences may be related to preferential selection of certain prey size classes or differences in the depths at which various species feed. Virtually nothing is known of the winter food habits of penguins or flighted seabirds that remain south of the Antarctic Convergence.

Feeding behavior

Antarctic seabirds partition resources by different feeding methods, vertical and horizontal segregation, and timing of feeding. Ainley et

Table 23. Percentage composition by weight of items in the diet of various Antarctic seabirds (From Croxall, 1984).

Species	Main prey classes					Crustacean prey				Locality	Reference
	Squid	Fish	Lamprey	Crustacea	Carrion	Euphausiids	Decapods	Amphipods	Copepods		
Adelie penguin	+	39		61		98[a]		2	+	Cape Crozier	Emison, 1968
Adelie penguin		+		100		100		+		S. Shetland I.	Volkman et al, 1981
Chinstrap penguin		4		96		100		+		S. Shetland I.	Croxall and Furse, 1980
Chinstrap penguin		+		100		100		+		S. Shetland I.	Volkman et al., 1981
Gentoo penguin		15		85		100		+		S. Shetland I.	Volkman et al., 1981
Gentoo penguin		32		68		100		+		South Georgia	Croxall and Prince, 1980[a]
Macaroni penguin		2		98		100		+		South Georgia	Croxall and Prince, 1980[a]
Macaroni penguin		25		75		75[b]		+		S. Shetland I.	Croxall and Furse, 1980
Black-browed albatross	21	38	1	40	+	95	2.5	2.5		South Georgia	Prince, 1980[b]
Grey-headed albatross	49	24	11	16		96	2	2		South Georgia	Prince, 1980[b]
Light-mantled sooty albatross	47	11		41	+	89	10	1		South Georgia	Thomas, 1982
Dove prion	1	2		97		60		8	32	South Georgia	Prince, 1980[a]
Broad-billed prion	1	2		97		6[c]	+	20		Chatham I.	Imber, 1981
Blue petrel	1	8		91		90	1	5	4	South Georgia	Prince, 1980[a]
White-chinned petrel	47	24		29		96	2	2		South Georgia	Prince, unpublished
Grey-faced petrel	58	28		12		17[e]	54	+		New Zealand	Imber, 1973
South Georgia diving petrel				100		76		4	20	South Georgia	Payne and Prince, 1979
Common diving petrel				100		15		17	68	South Georgia	Payne and Prince, 1979
White-faced storm petrel		30		70		67[d]		14	+	Chatham I.	Imber, 1981
Grey-backed storm petrel		+		100[t]		7[c]		7		Chatham I.	Imber, 1981

Euphausiids were all E. superba except [a] 99% E. crystallorophias, [b] 50% Thysanoessa macrura, [c] Nyctiphanes australis, [d] mainly N. australis and Nematoscelis megalopds; remaining crustaceans (9%) were brachyurans, stomatopods and mysids.

[e] Remaining crustaceans (28%) were mysids.
[t] 85% were larvae/juveniles of Lepas australis (Cirripedia).
+ Present in small quantities.

Table 24. Estimated average prey composition, by weight, of stomach contents of seabirds from localities of the South Pacific Ocean and Ross Sea[a]. (From Ainley et al., 1984).

Species	Deep ocean[b]			Continental slope[b]				Continental shelf[b]			
	C	S	F	C	S	F	O	C	S	F	O
Adelie Penguin				509.4 (97.7)		12.0 (2.3)		840.6 (99.9)		0.8 (0.1)	
Light-mantled Sooty Albatross	14.6 (100)										
Southern Giant Fulmar				21.9 (22.6)	72.0 (74.3)		3.0 (3.1)				
Southern Fulmar	21.2 (6.4)	311.6 (93.6)									
Cape Petrel	0.8 (2.9)	27.0 (97.1)									
Antarctic Petrel	4.4 (3.9)	114.5 (96.3)		10.4 (17.4)	39.4 (65.8)	10.0 (16.7)	0.1 (0.2)				
Snow Petrel	4.2 (34.4)	8.0 (65.6)		9.9 (36.8)	17.0 (63.2)			0.5 (1.1)	3.5 (8.3)	38.4 (90.6)	
Mottled Petrel	2.1 (0.7)	321.6 (98.4)	3.0 (0.9)								
Wilson's Storm-Petrel				1.2 (36.3)	1.5 (45.5)	0.5 (15.2)	0.1 (3.0)				
Arctic Tern	3.7 (100)										
South Polar Skua					120.0 (86.0)	19.5 (14.0)		0.3 (0.8)	8.0 (21.0)	28.8 (75.6)	1.0 (2.6)

[a] Diet composition expressed by weight in grams; percent composition given in parentheses. Data extrapolated from Tables 5, 6, 7, 9, 10.
[b] C = crustacean, S = squid, F = fish, O = other.

al. (1984) described a variety of feeding methods used by Antarctic seabirds (Table 25). Croxall (1984) noted several feeding behaviors used by surface-feeding species including seizing prey, while the bird floats at the surface; plunging, exhibited by terns; and surface diving, common among petrels. Vertical and horizontal segregation further define individual niches (Croxall and Prince, 1980a; Croxall, 1984) (Table 26). Diving species exhibit preferred feeding depths that differ among groups (Kooyman et al., 1971; Conroy and Twelves, 1972). Larger species of penguins dive to depths of up to 265 m, whereas some of the smaller petrels and less highly adapted species such as shags make shallower feeding dives. Lishman and Croxall (1983) recorded diving depths for chinstrap penguins of up to 70 m at Signy Island. Seabirds also partition food resources through different foraging ranges (Fig. 20); larger flighted seabirds can forage much farther afield from nest sites than the penguins (Croxall and Prince, 1983). Finally, the preferred time of day for feeding activities varies among different species (Ainley et al., 1984). For example, emperor penguins showed a peak feeding activity at 0900 - 1400 h whereas adelie penguins preferred 0300 - 0500 for feeding.

Role in the Ecosystem

The role of Antarctic seabirds in the marine ecosystem is one of considerable importance. Although much remains unknown about the distribution, abundance, and energetics of Antarctic seabirds, even rough estimates of biomass and potential prey consumption indicate the magnitude of these predators' impact in structuring the marine community. Croxall and Prince (1982) and Croxall et al. (1984) estimated the prey potentially consumed by the principal groups of seabirds (Table 27). Those figures indicate that the annual krill consumption by seabirds in the Scotia Arc area may be as high as 16 million metric tons. Considerable amounts of fish and squid are also consumed. Croxall (1984) estimated that seabirds throughout the Antarctic may consume as much as 115 million metric of krill annually. He noted that this amount was much more than the amount assumed to be eaten by whales and nearly two-thirds of the estimated annual krill consumption by seals. Hence, Antarctic seabirds clearly have an important ecological role in the marine community.

Table 25. Feeding behaviors of Antarctic seabirds. (From Ainley et al., 1984).

Species	Percent of Observations									
	Dip	Contact Dip	Patter	Pursuit Plunge	Dive	Surface Seize	Scavenge	Pirate	Total no. obs.	Percent near ice[a]
Southern Fulmar						100			6	0
Antarctic Petrel	7	40		20	6	21	3	3	71	11
Snow Petrel	35	55	2		4	4			55	69
Mottled Petrel				67		33			3	0
Wilson's Storm-Petrel	9	14	74			3			35	11
Black-bellied Storm Petrel			100						9	0
South Polar Skua		32				27	23	18	22	4

[a] Feeding in water within 1 m of ice floes.

Table 26. Feeding zones of Antarctic seabirds. (From Croxall, 1984).

	Inshore	Intermediate	Offshore	Intermediate	Pelagic
Diving	Gentoo penguin	Chinstrap penguin	Macaroni penguin Adelie penguin	King penguin	
	Diving petrels				
Surface feeding	Storm petrels		Black-browed albatross		Wandering albatross
	Diving petrels		Grey-headed albatross		Sooty albatrosses
	Giant petrels		Snow petrel		White-chinned petrel
	Antarctic skua		Antarctic fulmar		Grey-faced petrel
	Antarctic tern		Cape pigeon		Grey petrel
		Prions		Blue petrel	Kerguelen petrel
				Antarctic petrel	White-headed petrel

Fig. 20. The maximum estimated foraging ranges of seven species during chick-rearing. Estimated from swimming/flying speeds and duration of feeding trips at sea. The dotted lines are shelf-boundaries. (From Croxall and Prince, 1983).

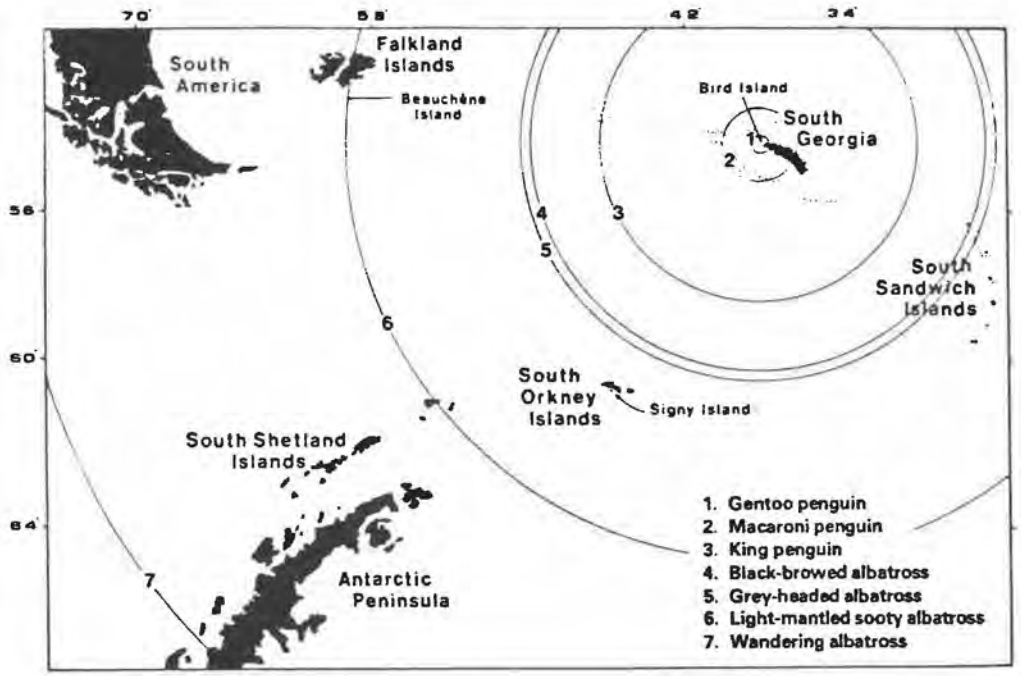


Table 27. Estimated food consumption (tons x 10^3) of seabirds in the Scotia Sea. (After Croxall et al., 1984).

Species	South Georgia	Rest	Total	Krill	Squid	Fish	Copepod	Amphipod	Others
King penguin *Aptenodytes patagonicus*	65.4		65.4		45.8	19.6			
Adelie penguin *Pygoscelis adeliae*		464.6	464.6	464.6					
Chinstrap penguin *P. antarctica*	2.5	3847.7	3850.2	3850.2					
Gentoo penguin *P. papua*	84.5	35.5	120.0	81.6		38.4			
Macaroni penguin *Eudyptes chrysolophus*	3917.1	7.8	3924.9	3806.5		78.5			
Wandering albatross *Diomedea exulans*	2.9		2.9	0.3	2.3	0.3			
Black-browed albatross *D. melanophrys*	21.7		21.7	8.3	4.6	8.5	0.2	0.2	
Grey-headed albatross *D. chrysostoma*	41.9		41.9	6.3	20.6	14.7		0.4	
Light-mantled sooty albatross *Phoebetria palpebrata*	4.9		4.9	1.8	2.3	0.6			0.2
Southern giant petrel *Macronectes giganteus*	3.3	11.4	14.7	11.7	2.0	1.0			
Northern giant petrel *M. halli*	2.3		2.3	1.5	0.6	0.2			
Antarctic fulmar *Fulmarus glacialoides*		640.3	640.3	544.2	96.0				
Cape pigeon *Daption capense*	3.6	179.6	183.2	155.7	27.5				
Snow petrel *Pagodroma nivea*	0.5	77.8	78.3	1 62.6	7.8	7.8			
Dove prion *Pachyptila desolata*	2319.7	26.4	2346.1	1360.7	23.5	54.6	727.3	187.7	
Blue petrel *Halobaena caerulea*	8.0		8.0	6.6	0.1	0.6	0.3	0.4	
White-chinned petrel *Procellaria aequinoctialis*	770.5		770.5	210.1	365.8	186.8		7.8	
Wilson's storm petrel *Oceanites oceanicus*	9.5	79.3	88.8	40.0	4.4	35.5	8.9		
Black-bellied storm petrel *Fregetta tropica*	0.5	2.2	2.7	1.3	0.1	1.1	0.3		
Common diving petrel *Pelecanoides u. exsul*	352.6		352.6	48.1			250.0	54.5	
South Georgia diving petrel *P. georgicus*	165.2		165.2	125.6			33.0	6.6	
Blue-eyed shag *Phalacrocorax atriceps*	4.7	8.4	13.1		1.0	11.3	0.3		0.5
Antarctic tern *Sterna vittata*	0.3	5.2	5.5	0.8	2.7	0.8	1.1		

CHAPTER 7: ANTARCTIC SEALS

Introduction

Reviews by Laws, (1964, 1977a, 1977b), Bonner and Laws (1964), Øritsland (1970, 1977), Ray (1970), Erickson and Hofmann (1974), Gilbert and Erickson (1977), and SCAR/SCOR (1983c) described the general biology and ecology of Antarctic seals. The excellent review by Laws (1984) has provided an up-to-date and comprehensive summary of current knowledge of Antarctic pinnipeds.

Species Composition

Eight species of seals occur in the waters south of the Antarctic Convergence. Of these, 4 are true Antarctic seals (crabeater seal, leopard seal, Ross seal, Weddell seal); 2 are sub-Antarctic seals (southern elephant seal and Antarctic fur seal); and 2 are transient species whose main distribution is north of the Antarctic Convergence (New Zealand fur seal and the sub-Antarctic fur seal) (Table 28). Because of their relatively small numbers and limited time south of the Convergence, New Zealand fur seals and sub-Antarctic fur seals are not considered in depth in this paper.

Distribution

The 4 true Antarctic seals have a circumpolar distribution. Crabeater, leopard, and Ross seals inhabit the pack ice zone whereas Weddell seals generally are associated with fast ice. Antarctic fur seals and southern elephant seals occur in the vicinity of sub-Antarctic islands and along the Antarctic Peninsula.

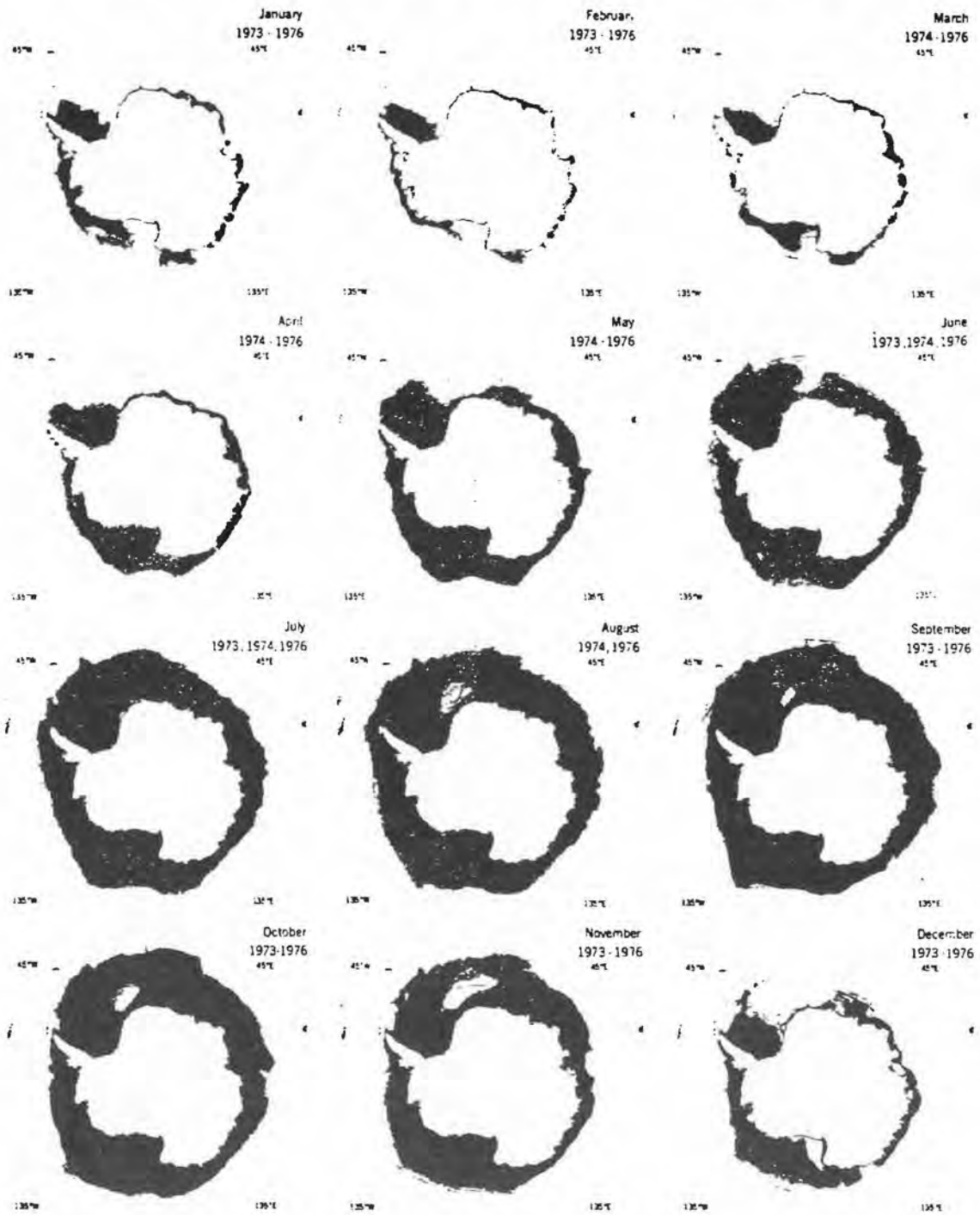
Crabeater Seals

Unconsolidated pack ice, covering 30% - 70% of the water surface, is apparently the preferred summer habitat of crabeater seals (Siniff et al., 1970; Erickson et al., 1971). Gilbert and Erickson (1977) found that this species is likely to be distributed relatively close to the edge of the pack ice in cake and brash ice of 7 to 8 octas concentration. This strong association with the pack ice edge accounts for a large seasonal movement from north to south as the pack ice zone fluctuates around the Antarctic continent (Fig. 21). Hence, as the ice edge is receding during the summer, crabeater seals move southward (Bertram, 1940; Turbott, 1952; Bonner and Laws, 1964; Solyanik, 1964). As sea ice forms in the autumn and the edge of the ice advances, crabeater seals apparently move north. In early spring, in the months of August through October, crabeater seals are present mostly along the northern perimeter of the ice edge (Øritsland, 1970; Siniff et al., 1977a; Siniff et al., 1978; Siniff et al., 1979).

Table 28. Pinnipeds and cetaceans found in waters south of the Antarctic Convergence.

GROUP	SPECIFIC NAME	COMMON NAME
PHOCIDAE	Lobodon carcinophagus	crabeater seal
	Hydrurga leptonyx	leopard seal
	Ommatophoca rossi	Ross seal
	Leptonychotes weddelli	Weddell seal
	Mirounga leonina	southern elephant seal
OTARIIDAE	Arctocephalus gazella	Antarctic fur seal
	A. tropicalis	sub-Antarctic fur seal
	A. forsteri	New Zealand fur seal
MYSTICETI	Family: Balaenopteridae	
	Balaenoptera musculus	blue whale
	B. musculus brevicauda	pygmy blue whale
	B. physalus	fin whale
	B. borealis	sei whale
	B. acutorostrata	minke whale
	Megaptera novaeangliae	humpback whale
	Family: Balaenidae	
	Balaena glacialis	right whale
ODONTOCETI	Family: Physeteridae	
	Physeter macrocephalus	sperm whale
	Family: Ziphiidae	
	Beradius arnuxii	Arnoux's beaked whale
	Hyperoodon planifrons	bottlenose whale
	Family: Dephinidae	
	Orcinus orca	killer whale
	Globicephala melaena	long-finned pilot whale
	Lagenorhynchus cruciger	hourglass dolphin
	Cephalorhynchus commersonii	Commerson's dolphin
	Family: Phoceonidae	
	Phoceona dioptrica	spectacled porpoise

Fig. 21. Satellite images of Antarctic sea ice. Distributions shown represent monthly mean values for 1973-1976 (from Zwally et al., 1983).



This annual north-south movement of the ice probably serves to concentrate the seals during periods of minimum ice cover. For example, in late February and March along the Antarctic Peninsula, dense groups of crabeater seals are commonly seen (Siniff et al., 1970). Up to 200 seals have been seen on one ice floe at that time of year (Bengtson, personal observation). February and March censuses by Siniff et al. (1970) revealed an average density of 1.6 seals/km^2. These aggregations of seals may be concentrated by the loss of suitable substrate as the pack ice edge recedes. In contrast, densities of crabeater seals in the spring are much lower. Siniff et al. (1979) observed a spring time density of 0.7 and 0.8 seals/km^2 in 1976 and 1977, respectively, in the Weddell Sea. Øritsland (1970) observed crabeater seals within a density range of 0.28 to 0.97/km^2. Individuals observed in the pack ice at that time of year are mostly breeding age individuals. They have presumably dispersed through the pack ice to undertake reproductive activities. The non-breeding segment of the population apparently remains together in concentrations that are found in fast ice bays (Siniff et al., 1979).

Whether the concentrated groups observed in the fall remain together during the winter is unknown; however, in spring dense concentrations are also seen occasionally (Siniff et al., 1977a; Siniff et al., 1979). Such groups, which have also been reported by Laws and Taylor (1957), Solyanik (1964), and Lindsey (1938), are known to include primarily juvenile animals or older females which did not breed in the past season (Fig. 22). Price (1980) reported the arrival and departure of over 200 crabeater seals at Signy Island in June, 1980.

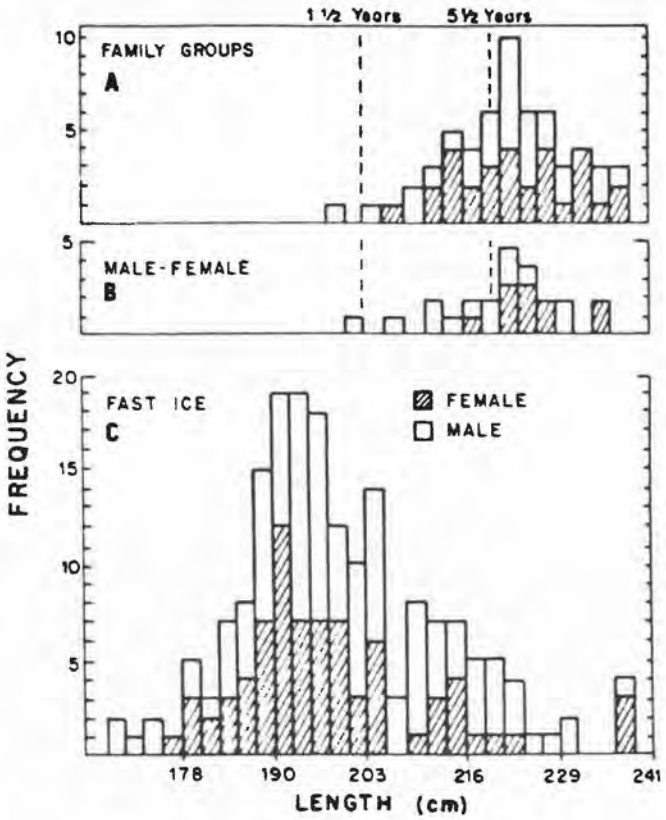
The presence of juvenile crabeater seals in aggregations may bepartially a response to predation by leopard seals, which is known to be significant (Siniff and Bengtson, 1977). Several authors have noted that weaned pups congregate in fast ice or dense pack ice areas near land (Lindsey, 1937; Bertram, 1940; Hofman, 1975). Stirling and Kooyman (1971) documented the arrival of sub-adult crabeater seals at McMurdo Sound near the end of summer. Young inexperienced seals may use this behavior as an anti-predator strategy when they are vulnerable to attacks by leopard seals.

Leopard seals

The distribution of leopard seals is similar to that of crabeater seals, perhaps due to the importance of krill and crabeater seals in its diet (Gilbert and Erickson, 1977). Although certainly primarily found in pack ice habitats, this species (particularly juveniles) occasionally hauls out on some of the sub-Antarctic islands (Kemp and Nelson, 1931; Hamilton, 1939; Bechervaise, 1963; Scheffer, 1958; Kooyman, 1981c).

Seasonal movements of leopard seals, as with crabeater seals, are apparently strongly correlated to fluctuations in pack ice cover. Seasonal fluctuations in the numbers of leopard seals have been reported around Palmer Station (Hofman et al., 1977) and Heard and Macquarie

Fig. 22. Length frequencies of individuals collected in the austral spring in (A) family groups, (B) male-female pairs, and (C) concentrations on fast ice. (From Siniff et al., 1979).



Islands (Rounsevell and Eberhard, 1980). Local seasonal movements and distribution near penguin colonies along the coasts of the Antarctic continent and adjacent waters has been documented by Bechervaise (1963), Penny and Lowery (1967); Øritsland (1970), Erickson et al. (1971), Muller-Schwarze and Muller-Schwarze (1971, 1975), and Dawson (1974). It is, however, difficult to ascertain whether these sightings are indicative of a widespread seasonal behavior pattern among leopard seals, or the result of biased sightings from land-based observers.

Ross seals

Ross seals are distributed in dense ice areas (Gilbert and Erickson, 1977) throughout the circumpolar pack ice. There appear to be areas of higher densities of Ross seals (King, 1964; Erickson et al., 1969, 1972; Erickson, 1971) especially between $6^{O}E$ and $6^{O}W$ (Condy, 1976).

On the basis of limited data, the breeding distribution appears to be widespread. Pups have been observed south of the Scott Islands (Tikhomirov, 1975), and near the South Shetland Islands (Solyanik, 1964; DeMaster et al., 1980). Seven fetuses were collected from females near the South Orkney Islands in September and October of 1964 (Øritsland, 1970). Possible seasonal movements of Ross seals are completely unknown, although they are thought to be influenced by seasonal fluctuations of pack ice.

Weddell seals

In contrast to the other ice seals, Weddell seals are associated principally with fast ice near the continent. Small breeding populations also occur in the South Shetland Islands, South Orkney Islands, South Sandwich Islands, and at South Georgia (Bonner, 1958; Laws, 1984). Their preferred pupping habitat is stable fast ice with predictable annual tide cracks (Stirling, 1969c; Siniff et al., 1977b; DeMaster, 1978). Non-breeding Weddell seals range into the pack ice, but no preference for a particular type of pack ice has been demonstrated (Gilbert and Erickson, 1977). Smith (1965) suggested that the majority of the McMurdo Sound population moved north into pack ice during the winter. Others contend that the population is resident throughout the winter (Lindsey, 1937; Bertram, 1940; Stirling, 1969c; Davis et al., 1982).

Fur seals

Bonner (1968, 1976, 1981) reviewed the distribution of the three fur seals which are found in Antarctic waters. Of these, the Antarctic fur seal (Arctocephalus gazella) is the most abundant and the only one that breeds primarily south of the Antarctic Convergence. Antarctic fur seals are distributed from the South Shetland Islands eastward to Heard Island and north to Prince Edward Island (Bonner, 1981) (Fig. 23). The principal breeding population is at South Georgia which, with the Willis Islands, served as the nucleus population for the recovery of the species following 19th century overexploitation. The breeding range of Arctocephalus tropicalis is north of the Antarctic Convergence from

Fig. 23. Distribution of Arctocephalus fur seals, circumantarctic species (from Bonner, 1968 and Repenning et al., 1971). (From Bonner, 1981).

Tristan de Cunha to Amsterdam Island. In the non-breeding season, individuals are known to come south of the Convergence and have been identified at South Georgia (Payne, 1979). The sub-Antarctic fur seal and the Antarctic fur seal overlap at Macquarie Island (Shaugnessy, unpublished data) and at Marion Island, where both are present in breeding groups and apparently hybridize (Condy, 1978b). The New Zealand fur seal Arctocephalus forsteri, breeds at New Zealand and south of New Zealand, but is known to occur on some of the sub-Antarctic islands such as Macquarie, Campbell, and Antipodes (Wilson, 1981).

Very little is known about the distribution of any of these species during the non-breeding, pelagic phase. Ainley (pers. comm.) has seen "fur seals in abundance" at sea as far south as the northern edge of the pack ice in the Scotia/Weddell Seas. Antarctic fur seals tagged at South Georgia have been sighted at the South Orkney Islands, the South Shetland Islands, and Tierra del Fuego (Hunt, 1973; Payne, 1979). Payne (1979) suggested that Antarctic fur seals may undertake a seasonal migration similar to the one exhibited by northern fur seals (Callorhinus ursinus) in the North Pacific. If such a migration occurs, it may have gone undetected due to the low population levels of fur seals since their exploitation in the 1800's (Laws, 1984).

Elephant seals

Southern elephant seals are distributed throughout the sub-Antarctic and southward along the Scotia Arc and the Antarctic Peninsula. The principal breeding sites are at South Georgia, Kerguelen, Heard, and Macquarie Islands (Laws, 1960a). Breeding sites are known as far south as Avian Island (Laws, 1960a; Muller-Schwarze et al., 1978) and Peterson Island near the Antarctic continent (Murray, 1981). Breeding and non-breeding indivioduals are occasional visitors to northerly continental areas as well (Ling and Bryden, 1981). The distribution of past and current breeding and non-breeding sites for elephant seals was described by Scheffer (1958) and Carrick et al. (1962).

The movements of southern elephant seals during the non-breeding season are generally unknown. However, sightings of tagged individuals as described by Laws (1984) indicate that these seals may range as far as 2400 km from their breeding grounds (Laws, 1960a; Dickenson, 1967; Ingham, 1967; Hunt, 1973; Scolero, 1976; van Aarde and Pascal, 1980; Murray, 1981).

Stock Discreteness

Evidence for discreteness of Antarctic seal stocks varies between species (Seal et al., 1971a, 1971b). An evaluation of protein polymorphisms indicated no intraspecific differences for crabeater, leopard, or Ross seals sampled in different areas, but some differences for Weddell seals (Seal et al., 1971a, 1971b; Hofman, 1975). The lack of fixed land or fast ice breeding sites for pack ice species may result in less isolation, leading to greater gene interchange between individuals in different geographic areas.

It is not clear from limited tagging work whether pack ice species make significant movements east to west. Two crabeater seals tagged along the Antarctic Peninsula were resighted in the same area two years later (Siniff et al., 1980). Likewise, Hofman and Flesness (pers. comm.) resighted a tagged leopard seal near Palmer Station where it had been tagged one year earlier. Whether these examples were representative of the population remains unproven, but these cases provided some evidence of area fidelity. The lack of observers outside of study areas probably biased the probability of resighting tagged seals.

There is evidence of discrete stocks of Weddell seals (Stirling, 1969b, 1971a) such as the population at White Island south of McMurdo Sound (Stirling, 1972). Protein polymorphisms in Weddell seals exhibit some differences between samples taken at distant localities around the Antarctic continent (Shaughnessy, 1969; Seal et al., 1971a, 1971b, Hofman, 1975). Furthermore, analyses of vocalizations has shwon that populations on opposite side of the continent have significantly different repertoires (Thomas and Stirling, 1983). The strong breeding site fidelity in Weddell seals (Stirling, 1969b, 1969c; DeMaster, 1978; Croxall and Hiby, 1983) is probably an important factor in isolating populations.

Although the degree of discreteness that may have been present in pre-exploited Antarctic fur seal stocks is unknown, present individuals apparently all are decendents of the small group of Antarctic fur seals which escaped exploitation at the Willis Islands near South Georgia (Bonner, 1964, 1968, 1981). An exchange of seals between areas currently occupied in the Scotia Arc is evident from tag returns (Payne, 1979; Hunt, 1973).

Although no differences were detected in protein polymorphisms in southern elephant seals (Seal et al., 1971b), there is no evidence of interchange between the 3 main breeding groups (Laws, 1984). Tagging studies have indicated only movements within these areas. Tagged elephant seals have traveled between South Georgia, the South Orkney Islands, South America, and the South Shetland Islands (Dickenson, 1967; Hunt, 1973; Scolero, 1976). Movements have also been recorded in the New Zealand sector between New Zealand, Campbell Island, Chatham Island, and Macquarie Island (Ingham, 1967). Finally, movements within the Kerguelen, Heard, and Marion Island group have been reported (van Aarde and Pascal, 1980).

Abundance

The abundance of Antarctic seals has been estimated differently for various species. Pup counts are most often utilized for fur seals, Weddell seals, and elephant seals, which breed at traditional sites on land or fast ice. For pack ice species, estimates are calculated from census transects supported by ship or aircraft (Laws, 1980; SCAR/SCOR, 1983c).

Ice seals

Despite the considerable logistical obstacles of censusing pack ice seals, several efforts have been made to estimate the size of these populations (Siniff et al., 1970; Erickson et al., 1971; Gilbert, 1974; Gilbert and Erickson, 1977; Hoshiai, 1981; SCAR/SCOR, 1983c; Ainley, 1984). Strip censuses flown from helicopters off U.S. icebreakers have formed the basis of many of these estimates. Surveys have concentrated on the 6 residual pack ice areas as identified by Gilbert and Erickson (1977) (Fig. 24). A variety of parameters affect these estimates, including activity patterns, haul-out rates, transect width, weather, light conditions, and ability to spot seals behind drift ice (Siniff et al., 1970; Erickson et al., 1971; Gilbert and Erickson, 1977). Laws (1980, 1984) reviewed recent census work, and a summary of recent population estimates is presented in Table 29 (SCAR/SCOR, 1983c).

Initial estimates of crabeater seal abundance at 5 - 8 million (Eckland and Atwood, 1962) probably underestimated the population because of different techniques. Moreover, there may have been smaller populations of crabeater seals at this time. Laws (1984) reviewed information from Beddington and Grenfell (1980) and Laws (1977a) suggesting an annual rate of increase for the crabeater seal population of approximately 7.5% over the past several decades. Laws speculated that a similar increase in abundance had occurred for leopard seals.

These assumed population increases thought to be a response to declining whale populations and the subsequent increase in krill availability. Indirect evidence of increased survival and growth rates from reproductive materials supports the idea that krill availability did indeed increase during this period (Bengtson and Laws, 1984). However, since 1962, there is evidence that crabeater seal growth rates along the Antarctic Peninsula slowed and age at maturity increased (Bengtson and Laws, 1984). These data suggest a potential leveling off in any population increase which may have been occurring (Bengtson, 1984).

Although censusing Weddell seals at breeding sites is relatively easy because it pups on fast ice (Siniff et al., 1977b), counts from many remote breeding sites are not available (DeMaster, 1979). It is not known whether the population sizes of Weddell seals has been changing. The local abundance of Weddell seals in the McMurdo Sound area was reduced during the early 1900's and the 1950's as this population was exploited to feed dog teams. In recent decades the population has apparently increased and is now relatively stable at approximately 2,500 (Stirling, 1971a,b; DeMaster, 1979). There are no data available from which potential changes in the abundance of Ross seals could be detected.

Fur seals and elephant seals

Antarctic fur seals were estimated to number from 1 - 2 million individuals prior to exploitation in the 19th century (Bonner, 1976). The unregulated slaughter of these seals, reducing their total population

Fig. 24. Six residual pack ice regions presumed to constitute population centers for pelagic Antarctic seal in the austral summer. (From SCAR/SCOR, 1983c). These regions were as follows:

A. Amundsen and Bellingshausen seas
B. Oates Coast
C. Wilkes Land
D. Queen Maud Land
E. Halley Bay
F. Weddell Sea

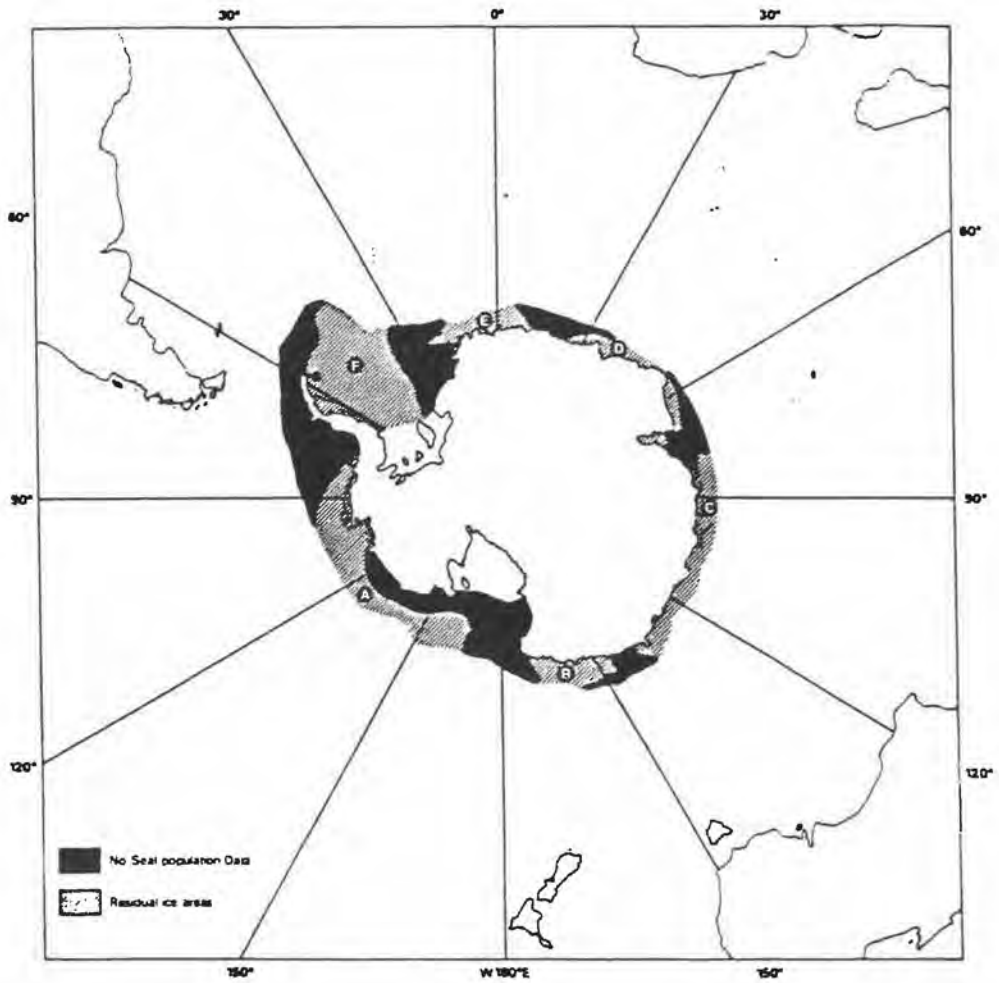


Table 29. Estimates of Antarctic seals in pack ice. Estimates from Erickson et al., 1970, 1974, 1983; Gilbert and Erickson, 1977; Siniff et al., 1970. (From SCAR/SCOR, 1983c).

Area and date	Crabeater	Leopard	Weddell	Ross	Total
Weddell Sea (68-69)	9 422 150	171 538	291 944	25 566	9 911 198
Amundsen/ Bellingshausen (71-72)	1 193 365	48 619	45 815	21 631	1 309 430
Oates and George V Coasts	472 424	23 194	64 869	63 964	624 451
Wilkes Land	1 179 849	86 860	49 462	16 889	1 333 060
Queen Maud Land	1 059 125	11 224	285 584	9 976	1 365 909
Halley Bay Region	1 093 702	63 503	20 978	22 413	1 200 596
	14 420 615	404 938	758 652	160 439	15 744 644

- Crabeater estimates were increased according to haulout rate correction factors
- Other estimates had no correction factors applied

to some tens or hundreds of individuals, has been well documented by Bonner (1964, 1968, 1981). Following the collapse of Antarctic sealing, stocks began to recover. This recovery has been reviewed by Bonner (1976), Laws (1977a, 1973), and Payne (1977, 1978). Population growth has been at a rate estimated to be between 15% and 17% annually (Laws, 1979). Concurrent with this increase in numbers, the recent geographic range of Antarctic fur seals has also been extended (Bonner, 1976). Fur seals have re-established breeding colonies in the South Orkney, South Sandwich, and South Shetland Islands as well as in other parts of their range (Paulian, 1952; O'Gorman, 1961; Holdgate, 1963; Aguayo and Torres, 1966; Holdgate et al., 1968; Budd, 1970; Erickson et al., 1970. The current population size of Antarctic fur seals is estimated to be over 1 million individuals (Table 30). These estimates are based on pup counts adjusted to include breeding females and males. The estimated abundance of sub-Antarctic fur seals is presented in Table 31.

Table 32 presents current population estimates for southern elephant seals (SCAR/SCOR, 1983c). In contrast to estimates for other Antarctic seal species, these estimates (of individuals that haul out) are known to be relatively accurate because of the relative ease with which these seals can be counted at accessible, known breeding sites. Elephant seals are increasing in some areas and decreasing in others (McCann, 1983). Condy (1978a) estimated a decline of approximately 69.5% at Marion Island between 1951 and 1976. A more recent evaluation (SCAR/SCOR, 1983c) indicates that elephant seals throughout the Antarctic and sub-Antarctic may be declining at a rate as high as 8% - 11% annually.

Social Organization and Reproductive Behavior

The social and reproductive behavior of the six Antarctic seals varies widely and is, in part, associated with breeding habitat and predatory pressure. Crabeater, leopard, and Ross seals inhabit an unstable area of constantly shifting pack ice. Weddell seals breed in areas of predictable fast ice, allowing association with specific sites. Elephant and fur seals have social systems adapted to female aggregation, terrestrial parturition, and seasonal breeding at specific sites on land.

Crabeater seals

Aspects of the social organization and reproductive behavior of crabeater seals have been described by King (1957), Øritsland (1970), Corner (1972), Siniff and Bengtson (1977), and Siniff et al. (1977a). Siniff et al. (1979) provided the most detailed description, and cited four social categories: family groups, male-female pairs, aggregations, and lone seals.

In the austral spring, pregnant females disperse throughout the pack ice zone, haulout on ice floes by themselves and deliver their pups. Females remain on the ice with their pups for the next 3 - 4 weeks, at which time the pup is weaned. During the suckling period, males search the pack ice for females and pups. When a male finds a female and pup, a

Table 30. Population estimates of Antarctic fur seal A. gazella. (From SCAR/SCOR, 1983c).

Area	Numbers Pups	Numbers Total	Trend	Reference
South Georgia	220×10^3	$1{,}09 \times 10^6$	↑	Payne, 1977; Doidge & Croxall, in prep.
South Orkney Islands	100	?	?	BAS, unpublished data
South Sandwich Islands	*	400	?	O'Gorman, 1961
South Shetland Islands	c.300	>6 600**	?	Aguayo, Maturana & Torres, 1977; Torres, unpublished data
Antarctic Peninsula	?	500**	?	Torres, unpublished data
Bouvet Island	>950	4 000	↑	Haftorn, Somme & Gray, 1981
Heard Island	300	4 000	↑	Johnstone, pers. comm.
MacDonald Island	100	300	?	Johnstone, pers. comm.
Iles Kerguelen	*	>1 800	↑	Bester 1981; Jouventin, Stahl & Weimerskirch, 1982
Iles Crozet (Possession Island)	*	20 ?	↑	Jouventin, Stahl & Weimerskirch, 1982
Marion Island	43	160	↑	Kerley, 1983
Prince Edward Island	30 ±	<200	↑	Kerley, 1983
Macquarie*** Island	< 20	< 50	↑	Johnstone, pers. comm.

* Present

** Almost all of these animals are probably migrants from South Georgia, and hence have already been included in the estimates

*** Both *tropicalis* and *gazella* are present, but identity of pups is unknown

Table 31. Population estimates of sub-Antarctic fur seal A. tropicalis. (From SCAR/SCOR, 1983c).

Area	Numbers		Trend	Reference
	Pups	Total		
Gough Island	53 076	200 000	↑	Bester, 1980
Tristan da Cunha Group	> 20	> 1 200	↑	Bester, 1980; Wace & Holdgate, 1976
Marion Island	3 813	19 857	↑	Kerley, 1983
Prince Edward Island	2 300	14 761	↑	Kerley, 1983
Iles Crozet (Possession Island)	> 58	300	↑	Jouventin, Stahl & Weimerskirch, 1982
Amsterdam Island	10 898	35 000	↑	Hes & Roux, 1983
St Paul Island	7		↑	Segozac, 1972
Macquarie Island*	20	50	↑	Johnstone pers. comm.

* Both *gazella* and *tropicalis* are present, but identity of pups is unknown

Table 32. Annual pup production and population estimates* of Southern Elephant seal M. leonina populations. (From SCAR/SCOR, 1983b).

Area	Number of pups born	Number of seals age 1+	Trend	Reference to pups borne
South Georgia	100 000	350 000	?	Laws, 1960
South Orkney Islands	< 100	< 350	↓	Laws, 1960; BAS unpublished data
South Shetland Islands	300	1 050	?	Muller-Schwarze et al., 1978 (derived)
Falkland Islands	1 000	3 500	↓	Laws, 1960
Gough Island	< 100	< 350	-	Bester, 1980
Patagonia	3 933	13 800	↑	Scolaro, 1976
Bouvet Island	**	350	?	Haftorn, Somme & Gray, 1981
Iles Kerguelen	45 000	157 500	↓	Pascal, 1979; van Aarde, 1980 (derived)
Heard Island	23 000	80 500	?	Carrick & Ingham, 1962
Marion Island	1 100	3 850	↓	Condy, 1979
Iles Crozet	c. 3 000	10 500	↓	Barrat & Mougin, 1978 (derived)
Amsterdam Island	?	25	?	Roux, unpublished data
Macquarie Island	39 000	136 500	?	Carrick & Ingham, 1962
Campbell Island	130	455	?	Sorenson, 1950

* Based on McCann (In press)

** Present

"family group" is formed. A male defends his female until she becomes receptive and copulation is completed. Family groups consisting of an adult female, her pup, and an adult male are present throughout the fringe of the pack ice in early spring. If other males arrive at a family group, the resident male defends his female and fights the challenger. These fights can be bloody, but usually end in the challenging male being chased away. Adult males apparently defend territories of up to 50 m in radius; males approaching closer than that distance are aggressively challenged (Siniff et al., 1979).

Upon pup weaning, family groups become "male-female pairs" as the male becomes dominant over the female (Siniff et al., 1979). During this time, males stay in physical contact almost constantly with females. Although males on ice floes have been observed attempting to mount females in a typical pinniped copulatory posture, actual copulation has not been seen. After a period presumed to be approximately 2 weeks, the male leaves the female, and the male-female pair bond dissolves. If dissolution of this pair bond occurs early enough in a season, a male may seek another mate and may be able to defend and inseminate a second female. Towards the end of October, single females are often seen in the pack ice. These seals are presumed to be post-parturient females that have been inseminated while in a male-female pair, and are now alone.

Aggregations of crabeater seals composed primarily of non-breeding individuals have been observed during spring by several authors (Laws and Taylor, 1957; Siniff et al., 1977a, 1979). At Admiralty Bay, King George Island, Siniff et al. (1979) found the majority of seals present in aggregations to be less than three years old.

Leopard seals

Leopard seals are mostly solitary inhabitants of the pack ice zone (Laws, 1964; Marlow, 1967; Øritsland, 1970; Siniff et al., 1970; Erickson et al., 1971). They are not known to form aggregations except for occasional small groups on ice floes (Hofman et al., 1977). Along the Antarctic Peninsula, females haul out alone in November and December, deliver their pups, and remain with them until weaning. The breeding behavior of males and females in the wild is unknown; copulation is presumed to occur underwater after pups have been weaned (Harrison et al., 1952; Harrison, 1969; Siniff et al., 1980). Copulation was observed to occur underwater between captive seals at the Sydney Zoo (Marlow, 1967). Observations of males in the vicinity of females with pups indicate that males apparently are not interested in females at that time; presumably courtship and mating takes place after weaning (Tikhomirov, 1975; DeMaster et al., 1980; Siniff, 1982).

Ross seals

The social organization of Ross seals is the poorest known of the Antarctic seals. As with leopard seals, solitary pregnant female Ross seals haulout onto ice floes and give birth. The only reported sightings

during this time are in the area of the South Orkney Islands (Valette, 1960), South Sandwich Islands (Solyanik, 1964), the Antarctic Peninsula (Thomas et al., 1980) and the Balleny Islands (Tikhomirov, 1975). Øritsland (1970) found fetuses in 7 of the Ross seals he collected west of the South Orkney Islands in September and October. There is no information on the breeding behavior of the species. Males have not been observed attending females and pups. Presumably pairing and copulation take place underwater after weaning of the pup.

Weddell seals

Weddell seal social organization and reproductive behavior is quite different than the pack ice species and has been described by Mansfield (1958), Stirling (1969a, 1971a), Smith and Burton (1970), Kauffman et al. (1975), Siniff et al. (1977b), and Croxall and Hiby (1983). In the austral spring, pregnant females haul out together at near-shore tide cracks in the fast ice. Females give birth to their pups in these colonies and suckle pups until weaning at approximately 6 weeks of age. During this time individual males patrol underwater territories adjacent to each other along the length of tide cracks, defending an opportunity to eventually copulate with receptive females entering their territories (Siniff et al., 1977b). Unlike the pack ice seals, lactating Weddell seals leave their pups periodically to feed. At approximately 2 - 3 weeks of age, pups join the mothers in the water (Stirling, 1969a).

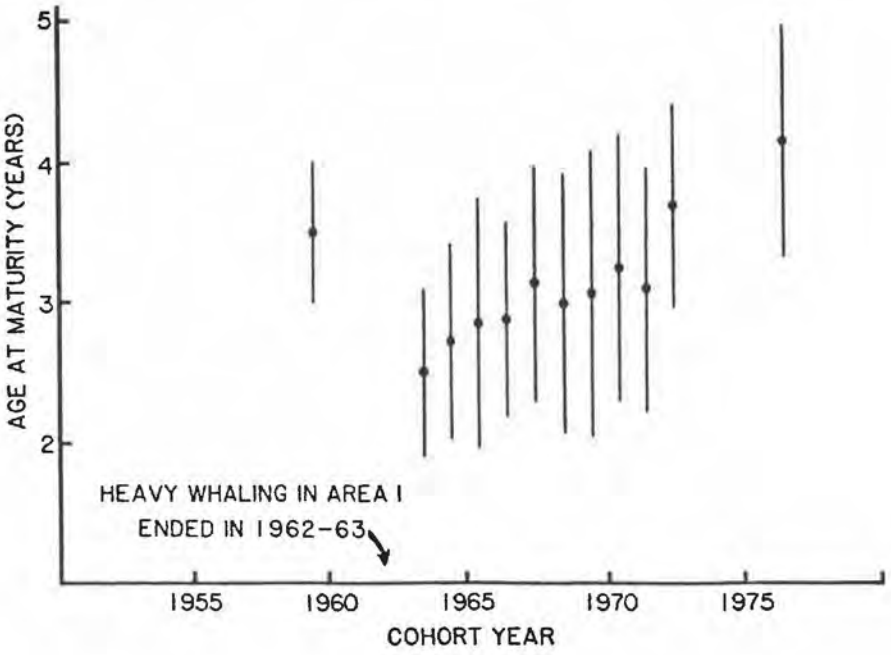
Three types of males are present in the vicinity of the pupping colonies during this time: transient males (mostly subadults) which stay in the area for a few days and then depart; basking males (adult but not yet dominant) which remain on the ice at some distance from the tide cracks (these include non-breeding males and wounded males recovering from underwater battles); and territorial males (fully dominant) which spend almost all of their time underwater defending territories (Siniff et al., 1977b). Just prior to pup weaning, females ovulate and copulate underwater with males (Kauffman et al., 1975).

Fur seals

Fur seals are polygynous. At South Georgia, mature males come ashore in late October to establish and defend territories. Females begin arriving ashore approximately 3 weeks later; they deliver their pups 1 - 2 days after they haul out (McCann, 1980b). Pupping is highly synchronous, with 90% born in a 3-week period (Payne, 1977). Of these, 50% are born by approximately 7 December (Payne, 1978). Females remain ashore for 5 - 8 days postpartum, copulate, and depart to sea for their first feeding trip during lactation (Doidge et al., 1983).

The lactation period continues for up to 115 days, during which time females make frequent trips to sea to feed. Trips last from 3 - 6 days with suckling periods ashore from 1 - 5 days (Bonner, 1968; Doidge et al., 1983; Doidge and Croxall, 1984; Bengtson et al., in prep.). Following copulation, males begin to abandon their territories and return

Fig. 25. Trends in crabeater seal age at maturity as estimated from ovarian corpora counts. Mean age ± 1 standard error are shown. (Data from Bengtson and Laws, 1984).



to sea until hauling out later in the season to molt. By early April, pups have been weaned and departed to sea.

Elephant seals

Elephant seals also form harems, but of a different sort than those of fur seals. Pupping and breeding usually occurs on land, but can also take place on fast ice. At South Georgia, bulls arrive ashore in September and are quickly followed by females which form groups. Females give birth approximately 8 days after hauling out and remain with their pups until weaning at approximately 3 weeks. Males defend their groups from other males with visual threats and occasional fights (Laws, 1956a, 1960a). McCann (1981b) stated that the majority of successful matings on a beach are performed by a minority of males. Copulation occurs during a 4-day receptive period in females occurring approximately 19 days postpartum (Laws, 1956, 1960a; McCann, 1980a).

Reproductive Biology

Crabeater seals

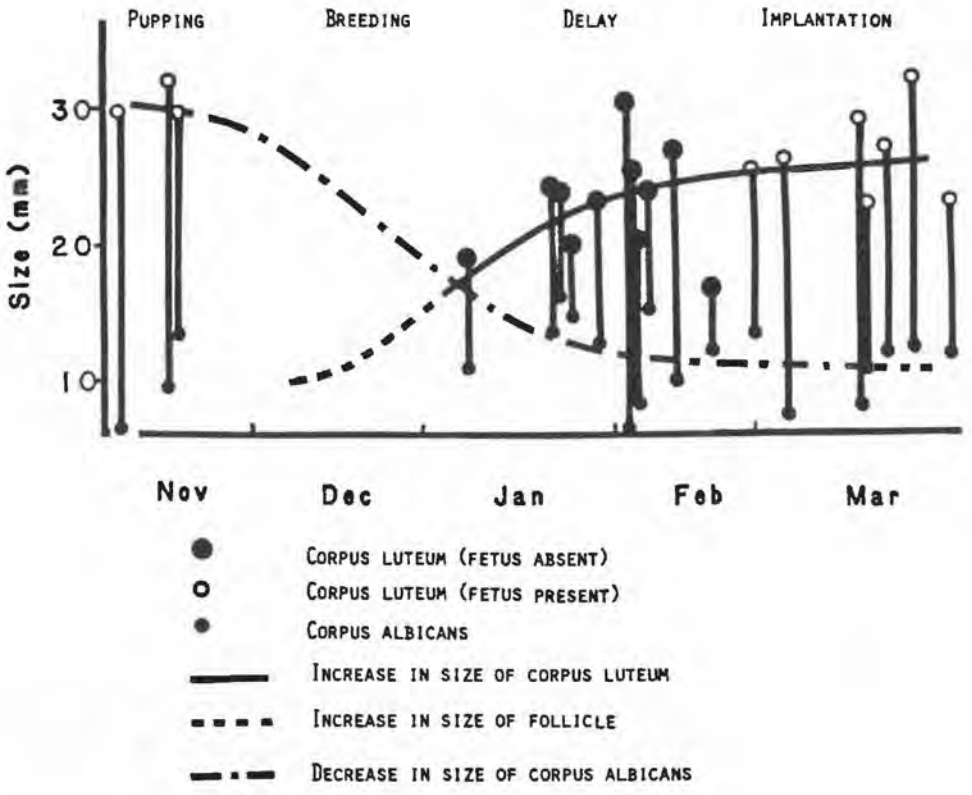
Bengtson and Siniff (1981) described reproduction in female crabeater seals from along the Antarctic Peninsula. They calculated an average age at sexual maturity of 3.8 years. Only females 5 years and older at age of insemination successfully carried fetuses full-term. As with the other Antarctic seals, females are capable of having one pup per year, although twinning does occur rarely (Øritsland, 1970; Bengtson and Siniff, 1981). Pups are weaned at approximately 3 - 4 weeks (Siniff et al., 1979). Younger seals ovulate later in the season than older seals, and no females ovulate prior to weaning their pups. Ovulation is presumed to occur primarily during the female's presence in a male-female pair. Implanted blastocysts are present in January (along the Antarctic Peninsula), indicating a delayed implantation of approximately 2 months (Bengtson, unpublished data).

The age at sexual maturity has been estimated at between 2 and 6 years of age (Laws, 1958; Øritsland, 1970; Tikhomirov, 1975; Bengtson and Siniff, 1981; Bengtson and Laws, 1984). It appears that within this range, age at maturity may vary according to density-dependent factors (Bengtson and Laws, 1984). These authors suggested that the age at maturity in crabeater seals along the Antarctic Peninsula had been increasing since 1962 in response to a decreasing availability of krill (Fig. 25).

Leopard seals

Reproduction in the leopard seal was investigated by Siniff and Stone (1984). Age at maturity has been estimated at 3 - 7 years in females and 2 - 6 years in males (Laws, 1957; Øritsland, 1970; Tikhomirov, 1975). Parturition occurs in October through December (Erickson and Hofman, 1974; DeMaster et al., 1980), followed by fertilization and a 2-month

Fig. 26. The reproductive cycle of the leopard seal showing size of the corpus luteum and largest corpus albicans for individual specimens. Large dots = corpus luteum (fetus absent); small dots = corpus albicans; circles = corpus luteum (fetus present). Solid line traces increase in size of corpus luteum (following increase in size of follicle) and broken line traces decrease in size of corpus albicans. (From Siniff and Stone, 1984).



delayed implantation (Sinha and Erickson, 1972; Siniff and Stone, 1984) (Fig. 26).

Ross seals

Øritsland (1970) estimated the age at maturity for females and males as 3 - 4 and 2 - 7 years, respectively. Tikhomirov (1975) estimated a range of 3 - 5 years for age at maturity in both females and males. Information on the timing of parturition in Ross seals is limited, but appears to be from mid-November to early December (Øritsland, 1970; Tikhomirov, 1975; Thomas et al., 1980).

Weddell seals

Age at maturity in Weddell seals has been estimated at between 3 - 6 years for females (Mansfield, 1958; Stirling, 1971a; DeMaster, 1979; Siniff, 1982; Croxall and Hiby, 1983). Males apparently become physiologically mature at a similar age, but do not become socially mature until 7 or 8 years of age (DeMaster, 1979). Timing of parturition varies depending on latitude. At Signy Island, mid-August is the average parturition date (Smith and Burton, 1970). In the southern Ross Sea, most pupping occurs in late October (Lindsey, 1937; Stirling, 1969a).

Fur seals

Payne (1977) indicated that most females at South Georgia pup for the first time at 3 years of age. Although it is not certain at what age males become sexually mature physiologically, they do not become socially mature until approximately 8 years of age (Laws, 1984). At South Georgia, females pup in early December (Bonner, 1968), ovulate and copulate 5 - 8 days postpartum (Bengtson and Schneider, 1983), and have a delayed implantation of at least 3.5 months (Bengtson, unpublished data).

Elephant seals

Female elephant seals pup for the first time at ages 3 - 5 years at South Georgia and 4 - 7 years at Macquarie and Heard Islands (Carrick and Ingham, 1962; McCann, in press). Males apparently become mature at 4 years, but do not become socially active until 6 years old (Laws, 1956). At South Georgia, the peak pupping period for elephant seals is in mid to late October (McCann, 1981a, 1981b). Copulation occurs approximately 19 days after parturition followed by a period of delayed implantation of about 4 months (Laws, 1956, 1960).

Food Habits

Understanding the feeding ecology of Antarctic pinnipeds is essential for delineating the role of this important group upon the marine ecosystem. The reviews by Øritsland (1977) and Laws (1977b) provided a synthesis of available food habits data. Table 33 updates their calculations with recent estimates of stock sizes and prey selection.

Table 33. Rough estimates of food consumption of Antarctic seals. Feeding rate estimated at 7% of body weight for all seals except elephant seals, which were assumed to consume 6% of body weight daily. Elephant seals were assumed to feed 290 days/year, all others 335 days/year. Modified from Øritsland (1977) and Laws (1977b) with data from SCAR/SCOR (1983c) and Siniff and Stone (1984). The units mt indicate metric tons.

Species	Stock size ($\times 10^3$)	Mean wt (mt)	Antartctic biomass ($\times 10^3$ mt)	Individual consumption Kg/ day	Individual consumption Mt/ year	Average food item frequencies (percentages in parentheses)[c] and annual consumption of stocks (millions of metric tons) Euphausiids	Cephalopods	Other invertebrates	Fish	Birds	Seals	Total
Crabeater	30000[a]	.193	5790.0	14	4.53	127.74 (94)	2.72 (2)	1.36 (1)	4.08 (3)	---	---	135.90
Leopard	400[a]	.272	108.8	19	6.38	1.15 (45)	.13 (5)	---	.13 (5)	.25 (10)	.89 (35)	2.55
Ross	220[b]	.173	38.1	12	4.05	.08 (9)	.57 (64)	.04 (5)	.20 (22)	---	---	.89
Weddell	730[b]	.246	179.6	17	5.77	.04 (1)	.46 (11)	1.48 (35)	2.23 (53)	---	---	4.21
Elephant	741[a]	.500	370.5	30	8.70	---	4.84 (75)	--	1.61 (25)	---	---	6.45
Ant. fur	1108[a]	.050	55.4	3	1.17	.44 (34)	.43 (33)	--	.43 (33)	---	---	1.30
All	33199	---	6542.4	--	----	129.45	9.15	2.88	8.68	.25	.89	151.30

a: Stock estimates from SCAR/SCOR (1983c)
b: Stock estimates from Gilbert and Erickson (1977)
c: Percentages for leopard seals from Siniff and Stone (1984), for leopard seals; from Øritsland (1977) for crabeater, Ross, and Weddell seals; and from Laws (1977b) for elephant and Antarctic fur seals.

The recent review by Laws (1984) describes the prey taken by different Antarctic pinnipeds (Table 34).

Crabeater seals

The crabeater seal diet consists primarily of krill (Laws, 1977a; Øritsland, 1977). The species' adaptation for specialist feeding on Antarctic krill can be seen in its finely-divided dentition which forms a sieve when the jaws are closed. Øritsland (1977) reported 94% of the diet to be krill, 3% fish, 2% cephalopods, and 1% miscellaneous invertebrates. Bengtson (1982) found that of 68 stomachs containing food items, all but one included some krill. Two of these had fish remains present and one had a small unidentified clam mixed with sand in the stomach.

Leopard seals

Leopard seals take a variety of prey including krill, squid, fish, penguins, and seals. Although the leopard seal has been widely reported as an important penguin predator (Brown, 1957; Penney and Lowry, 1967; Muller-Schwarze, 1971; Muller-Schwarze and Muller-Schwarze, 1971, 1975; Dawson, 1974), it is clear that it is an important predator on several other species as well (Tikhomirov, 1974; Hofman et al., 1977; Øritsland, 1977; Siniff and Bengtson, 1977; Siniff et al., 1979; Siniff, 1981; Stone and Meier, 1981; Bengtson, 1982; Siniff and Stone, 1984). Several authors have specifically called attention to the importance of Antarctic krill in the diet of leopard seals (Hofman et al., 1977; Øritsland, 1977; Bengtson, 1982; Siniff and Stone, 1984). Hamilton (1939) and Laws (1964) listed fish and squid as components of the leopard seal diet.

Siniff and Stone (1984) were able to identify seasonal shifts in the prey composition of leopard seals (Fig. 27). Other seals constitute important prey items for leopard seals (Wilson, 1907; Bertram, 1940; Laws, 1964; Gilbert and Erickson, 1977), including fur seals (Rankin, 1951), and Weddell and crabeater seals (Mawson, 1915; Hamilton, 1939; Mackintosh, 1967; Erickson and Hofman, 1974; Siniff and Bengtson, 1977; Siniff et al., 1979; Bengtson, 1982). Laws (1984) citing data from Stone and Siniff (1983) and Øritsland (1977), calculated the relative proportion of the leopard seal diet as: 50% krill, 20% penguins, 14% seal, 9% fish, and 6% cephalopods (Table 35).

The importance of other seals in the diet of leopard seals, described by these authors, supports the observations of Condy (1976), Siniff and Bengtson (1977), Siniff et al. (1979), and Siniff (1982) who emphasized the high rate of scarring of crabeater seals. These authors found a predominance of leopard seal scars on as many as 83% of the crabeater seals encountered. From the presence of fresh wounds on crabeater seals it is apparent that leopard seals mostly attack crabeater seals during crabeaters' first year of life (Fig. 28).

Table 34. Food items recorded from the stomachs of Antarctic seals. (After Laws, 1984).

	Weddell	Crabeater	Leopard	Ross	Elephant	Fur
Crustacea	Euphausia superba (E. crystallorophias) Antarctomysis ohlini (A. maxima) Cirolana sp. Epimeria sp. Eusirus microps Chorismus antarcticus Crangon antarcticus Isopods[4] Amphipods[4]	E. superba (E. crystallorophias)	E. superba (E. crystallorophias)	Amphipods[1] E. superba	Amphipods Nectocarcinus antarcticus	E. superba[2] (E. crystallorophias)
Cephalopoda	Psychroteuthis glacialis Paralodone charcoti Moroteuthis knipovitchi[4] Kondakovia longimanna[4] ?Crystalloteuthis sp.[4] Brachioteuthis picta[4] Gonatus antarcticus[4] Octopod sp.	"Octopus" Gonatus antarcticus	"Octopus" "Squid"	"Octopus" "Cuttlefish" Moroteuthis sp.[1] Onychoteuthid sp.[1] Degopsid spp.[1]	Cephalopods[5,6,7,8] Architeuthidae[9] Onychoteuthidae Gonatus antarcticus[10] Moroteuthis knipovitchi[10] Kondakovia longimanna[10] ?Psychroteuthis sp. ?Crystalloteuthis sp.[10] Octopodidae[10]	Ommastrephidae[2] (probably Stenoteuthis or Dosidicus) Onychoteuthidae (probably Onychoteuthis banksi)[2] Enoploteuthidae[2]
Other Invertebrates	Lamellibranch Holothurian Ribbon worms[3]		Lamellibranch Ascidian		Small sea creatures[6] Lamellibranchs[8] Brachiopods	
Pisces	Notothenia coriiceps Pleurogramma antarcticum Dissostichus mawsoni Cryodraco antarcticus Pagetopsis macropterus Gymnodraco acuticeps Trematomus sp.[12] Chaenocephalus aceratus Elasmobranchs	"Small fish" Paralepididae Chaenichthys sp.	Paralepsis atlantica	Myctophidae Bathydraconidae	Notothenia sp.[5] Flounders[11] Fish [6,7] Notothenia coriiceps[8]	Notothenidae[2] Notothenia rossii?[2]
Aves			Aptenodytes forsteri A. patagonica Pygoscelis adeliae P. antarctica P. papua Eudyptes robustus[14] Spheniscus magellanicus[15] Macronectes sp. Pelecanoides sp. Halobaena coerulea Pachyptila sp. Pelecanoides urinatrix Phalacrocorax atriceps[16] Daption capensis[17] Larus dominicanus[17] Tern spp.[18]			Pygoscelis papua Eudyptes chrysolophus[13]
Monotremata			Ornithorynchus anatinus[16]			
Mammalia	Blubber[4]		Lobodon carcinophagus Leptonychotes weddelli Mirounga leonina Arctocephalus gazella[16] Otaria flavescens[19]			

Notes: Except where otherwise stated the references are given in Ortiz-Land's (1977) review; parentheses, probable occurrence.
1. King (1969); 2. Bonnaire (1968); 3. Taldeyva (1958); 4. Clarke and Macleod (1982b); 5. Ling and Bryden (1981);
6. Csordas (1965); 7. Murphy (1914); 8. Laws (1965a); 9. Matthews (1929); 10. Clarke and Macleod (1982a); 11. Sorensen
(1950); 12. Kooyman (1981d); 13. Bonner and Hunter (1982); 14. Horning and Fenwick (1976); 15. Markham (1971);
16. Kooyman (1981b); 17. Raley (1954); 18. Roberts (1951); 19. Hamilton (1934).

Fig. 27. Frequency of occurrence (%) of food items in the stomachs of leopard seals in relation to time of year. Sample sizes and sources of data, as follows: Sept. - Oct., n = 38 specimens with food in stomachs, from Øritsland (1977); pooled data for Oct. - March, n = 39 specimens with food, from Tikhomirov (1975) not broken down by month; n = 66 specimens with food. (From Siniff and Stone, 1984).

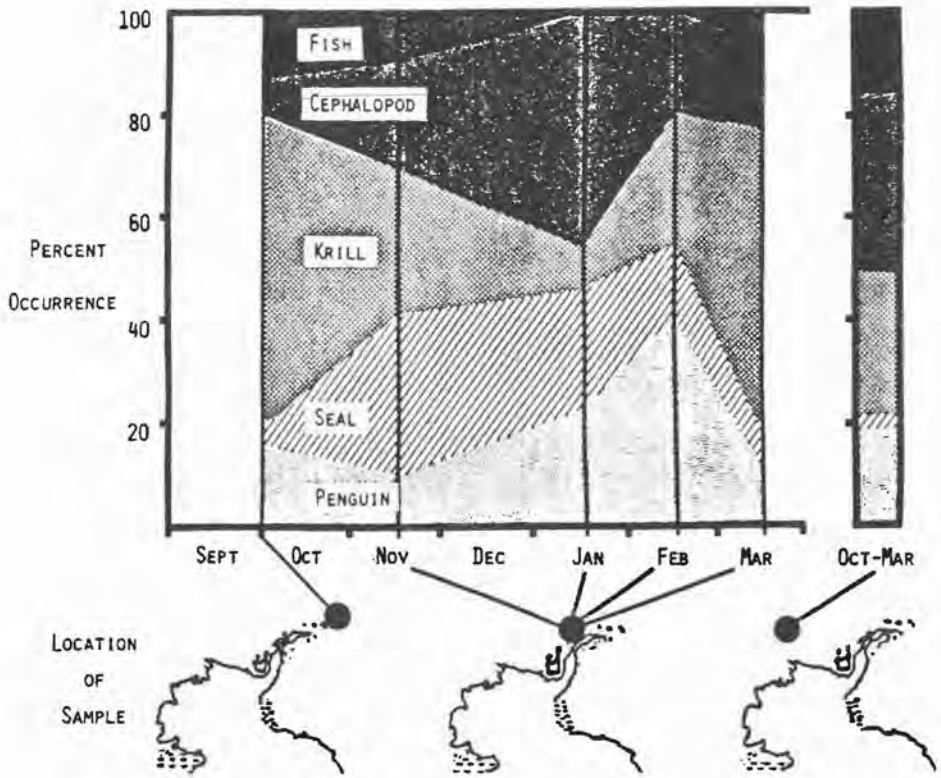
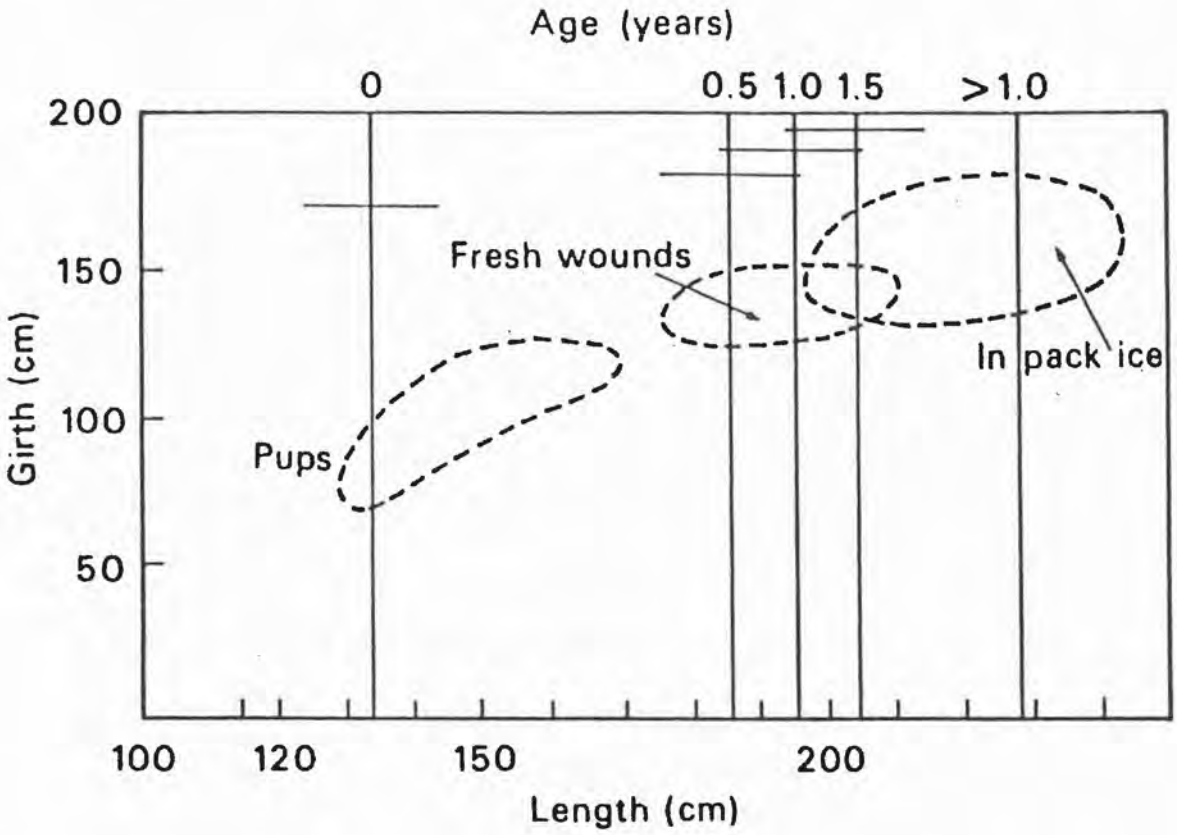


Table 35. Percent composition of leopard seal diet. Number of stomach examined that had some contents are indicated (n).

Prey type n =	Øritsland (1977) 38	Bengtson (1982) 14	Stone and Siniff (1983) 68	Laws (1984) --
Krill	58	43	45	50
Penguin	16	36	10	20
Seal	3	21	35	14
Fish	12	--	5	9
Squid	9	--	5	6

Fig. 28. Ellipses of plots of length against girth for crabeater seals. Mean lengths S.D. ± 1 are shown for age groups 0, 0.5, 1.0, 1.5 years and all seals > 1.0 year old (redrawn from Siniff et al., 1979). (From Laws, 1984).



Ross seals

The diet of Ross seals is poorly known. Cephalopods appear to be an important component of the diet, although fish and krill have also been found in Ross seal stomachs (Barrett-Hamilton, 1901; Wilson, 1907; Brown, 1913; Solyanik, 1964) (Table 34). King (1969) suggested that Ross seals may take larger squid (up to 7 kg in size) than do other seals. Supporting this idea are adaptations which apparently allow Ross seals to swallow large prey (Pierard and Bisaillon, 1979). Nevertheless, most of the squid found in Ross seal stomachs by Øritsland (1977) were small.

Weddell seals

Analysis of the stomach contents of Weddell seals indicates that a variety of prey are taken, including fish (Dearborn, 1965; Calhaem and Christoffel, 1969), squid (Clarke and Macleod, 1982b), and crustacea including Antarctic krill (Lindsey, 1937; Bertram, 1940). Of 8 stomachs from Weddell seals taken at Deception Island, the majority contained fish as well as teleosts, elasmobranchs, crustacea, isopods, amphipods, and Antarctic krill (Clarke and Macleod, 1982b). All the stomachs contained stones, as is common in leopard and crabeater seals (Bengtson, 1982). Clarke and Macleod (1982b) suggested that a seasonal shift in prey composition occurs from squid in March to octopods by July. Lipinski and Woyciechowski (1981) reported cephalopods in the stomachs of Weddell seals from King George Island, South Shetland Islands. These data, although not conclusive, support the suggestion by Kooyman (1981c) that Weddell seals along the Antarctic Peninsula may feed more heavily on cephalopods than Weddell seals in McMurdo Sound, for which fish such as Dissostichus mawsoni are important prey.

Fur seals

The lack of information on fur seal behavior during its pelagic phase confounds the determination of its principal prey items. However, it is clear that during the breeding season, Antarctic krill is a staple food of lactating females (Doidge and Croxall, 1984; Croxall and Pilcher, in prep.). Fish and squid are taken by juvenile and non-breeding adults (Bonner, 1968; North et al., 1983). Bonner (1968) noted that the specialization of the post-canine teeth suggests that squid may be an important element in the fur seal diet. Bonner (1981) also reported squid beaks, fish, and penguin remains in fur seal stomachs. Bonner and Hunter (1982) described the kill of a macaroni penguin at South Georgia and noted that fur seals occasionally took penguins. Laws (1977b) concluded on the basis of available information that krill, cephalopods, and fish each composed approximately one-third of the fur seal diet.

Elephant seals

As with fur seals, there is essentially no information on the pelagic food habits of elephant seals. Most food habits studies have been conducted during the molt period when elephant seals are mostly ashore

fasting (Laws, 1977a). It seems likely, however, that cephalopods comprise an important, if not major, part of the elephant seal diet. Laws (1956) noted that young elephant seals may feed on amphipods for a short time after weaning and that fish such as Notothenia are occasionally taken. Of the 139 stomachs he examined that contained food, 83% had cephalopods and 26% had fish remains present. Murphy (1914) and Matthews (1929) found a predominance of cephalopod beaks and some fish remains in elephant seal stomachs. Clarke and Macleod (1982a) examined 11 stomachs of elephant seals taken between November and May at Signy Island. Cephalopod beaks were the only identifiable food item in those stomachs. It is unknown how long such beaks persist in elephant seal stomachs, so it is difficult to estimate the relative importance of these remains in the seals' annual diet. The conclusion by Laws (1977b) and McCann (1983), that cephalopods constitute approximatey 75% and fish 25% of the elephant seal diet, seems to be the best estimate that can be made with the data currently available.

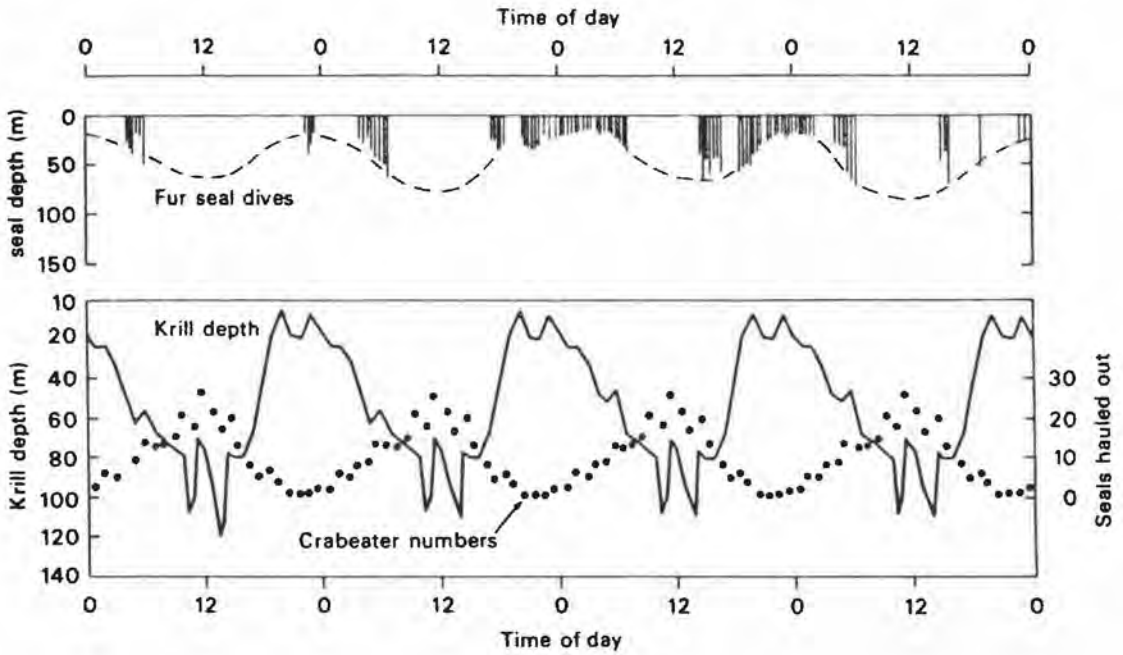
Feeding behavior

The depth of feeding dives and timing of feeding activity differ among the 6 Antarctic seal species. Ross, Weddell, and elephant seals are thought to feed at great depths, up to several hundred meters, with diurnal patterns that may vary seasonally (Laws, 1984). Crabeater, leopard, and fur seals utilize upper portions of the water column, probably about 60 - 80 m in depth. On the basis of crabeater seal haul out patterns (Erickson et al., 1971; Condy, 1977b; Gilbert and Erickson, 1977), Laws (1984) suggested that crabeater seals feed primarily at night when krill are closest to the surface (Fig. 29). He also suggested that leopard seals may follow this pattern. Using data on leopard seal diving behavior from Hofman et al. (1977), Laws (1984) estimated average depths of diving at about 56 - 81 m for leopard seals and crabeater seals, respectively, during a time when both were presumed to be feeding on krill.

The diving behavior of fur seals has been investigated by Kooyman and Davis (1980) and Kooyman et al. (in press) who used time/depth recorders to monitor feeding dives. They found that most diving activity was at night when krill were closest to the surface and most accessible. Most dives were between 20 - 50 meters in depth, with a maximum depth of 100 m (Fig. 29).

The diurnal haul out pattern for Weddell seals has been studied by several authors (Stirling, 1969c; Erickson et al., 1971; Kauffman et al., 1975; Gilbert and Erickson, 1977; Thomas and DeMaster, 1983). These authors found that most aquatic activity takes place during the night, although there is a seasonal shift related to photoperiod and breeding season. During feeding sessions, Weddell seals are known to dive to great depths (Kooyman, 1981c). At McMurdo Sound, dives of 2 - 400 m were frequent and one dive was measured to 600 m. Weddell seals may be capable of diving even deeper (the 600 m dive was essentially to the sea floor). The depths to which Weddell seals dove were the same depth at

Fig. 29. Diagrammatic representation of typical fur seal diving patterns over four days in January, data kindly provided by Kooyman; compared with diurnal variation in mean depth of krill in Scotia Sea in summer (from Chapter 10, Fig. 1), and diurnal variation in crabeater seal numbers hauled-out on pack ice on 21, 23, 25 January at about 69°S 4°E (data from Condy, 1977). (Lower plots are repeated over four days for comparison with diving pattern). (From Laws, 1984).



which Dissostichus mawsoni were commonly caught. The presence of fish in 97% of the stomachs examined containing food in McMurdo Sound (Dearborn, 1965) supports the idea that seals were diving to these depths to catch fish.

Ross seals are also thought to be deep divers, although information is very limited. Their oversized eyes, as well as the presence of large squid in their stomachs (King, 1969) suggests that Ross seals may be adapted for feeding at great depths. These seals appear to have a mid-day haul out peak, indicating a nocturnal feeding habit (Condy, 1977b; Gilbert and Erickson, 1977).

The feeding behavior of elephant seals is essentially unknown. Laws (1984) suggested three reasons why elephant seals probably feed deep in the water column. First, he felt it likely that Southern elephant seals are very similar to northern elephant seals which take prey species found at 100 - 300 m. Second, southern elephant seals take prey similar to sperm whales, which feed at great depth. Third, their eyes have a deep sea rhodopsin similar to that found in deep-water fishes and which has been suggested as an adaption for detecting the bioluminescence of deep-water squids (Lythgoe and Dartnall, 1970).

Ecological Partitioning

Each of the 6 Antarctic pinniped species differs from the others in its spatial and temporal utilization of resources (Table 36). Of the 4 ice seals, only 3 are prevalent in the pack ice zone. Moreover, Ross seals appear to prefer dense ice farther away from the pack ice edge where crabeater and leopard seals are found. These latter 2 species and perhaps Ross seals move seasonally with the advancing and retreating ice edge. The fourth ice seal, the Weddell seal, primarily utilizes stable fast ice areas in higher latitudes. Fur seals and elephant seals breed principally on land in lower latitudes. Hence, during their respective breeding seasons, the species are segregated among land, pack ice, or fast ice areas.

There are vertical differences in the spatial use as well. Fur seals, crabeater seals, and leopard seals apparently feed at shallower depths than do Ross seals, elephant seals, and Weddell seals. Finally, differences in feeding behavior, ranging from the specialist crabeater seal to the generalist leopard seal, emphasize the diversity within this important group of predators and the manner in which resources are partitioned within the Antarctic marine ecosystem.

Table 36. Ecological separation of Antarctic seals, promoted by geographical distribution, habitat preferences and food habits. (After Laws, 1984).

SPECIES	DISTRIBUTION			FEEDING		
	Breeding	Non-breeding				
		Summer	Winter	Teeth	Food	Depth
Fur seal	Land; colonial sub-Antarctic islands; maritime Antarctic, South Shetlands. Rocky coasts. Beaches-boulders or large pebbles	Dispersal north (to S. America?) and south to pack ice edge	Northward dispersal at sea	Canines large post-canines reduced	krill, fish and cephalopods	To 70 m for krill, probably deeper for cephalopods and fish
Elephant seal	Land; colonial South America, Falkland Islands, sub-Antarctic islands; maritime Antarctic. Beaches-sand or small pebbles	Dispersal north to South America and south to pack ice edge	Northward pelagic dispersal	Canines large; post-canines reduced	Cephalopods and fish	To 300 m or more; possibly unlimited
Leopard seal	Sub-Antarctic; Falkland Islands; South American coasts. Pack ice medium-sized hummocked floes. Female and pup	Pack ice periphery; sub-Antarctic and Cold Temperate islands and coasts. Southward shift	Pack ice periphery, and sub-Antarctic and Cold Temperate islands and coasts. Northward shift	Canines large post-canines large; multi-cusped	Krill, fish, cephalopods, penguins and seals	Mainly shallow, ? to c. 70 m for krill ? deeper for fish and cephalopods
Crabeater seal	Pack ice periphery - medium-sized hummocked floes. Triads, mated pairs. Immatures often on fast ice	Pack ice - cake and brash ice	Pack ice periphery	Canines small; post-canines large; multi-cusped	Krill	Shallow; ? to c. 70 m
Ross seal	Pack ice - probably as leopard seal	Dense pack ice - large floes	Pack ice	Canines very small, sharp; post-canines very small	Cephalopods	Deep
Weddell seal	Fast ice or land; colonial	Dispersal to pack ice near coasts or on fast ice	Fast ice, and pack ice nearby	Canines large; incisors procumbent; post-canines reduced	Fish, cephalopods, benthos	To 600 m or more; possibly unlimited

CHAPTER 8: ANTARCTIC WHALES

Introduction

Prior to commercial exploitation during this century, the Antarctic whales comprised perhaps one of the largest mammalian stocks ever to have existed on earth. Within a few short decades those abundant stocks were decimated, endangering the existence of several species, and very likely changing the composition and structure of the Antarctic marine ecosystem itself. By analyzing southern whaling and its ecological impacts, perhaps we will become better equipped to wisely manage future utilization of Antarctic marine living resources.

Species Composition

Seven species of baleen whales and 8 species of odotocete whales occur seasonally south of the Antarctic Convergence (Table 28). Ironically, the intensive commercial whaling of southern baleen whales was in large measure the reason that so much information is available about this group. The existence of a "dwarf" form of killer whale (Orcinus nanus) in the southern hemisphere has been suggested (Mikhalev et al., 1981; Berzin and Vladimirov, 1983), but this classification is not universally accepted. Evans et al. (1982) described pigmentation variations which suggest a distinct population of killer whales inhabiting ice edge and ice lead habitats.

Distribution and Migration

Baleen whales are mostly migratory, as evidenced by seasonal trends in abundance, direct observation of migration, or tagging studies (Mackintosh, 1965; Dawbin, 1966; Lockyer and Brown, 1981). Marking of individuals has documented extensive north-south movements (Brown, 1962a, 1977a). Whales migrate from their winter breeding grounds in subtropical and temperate waters to Antarctic waters for the summer where intensive feeding takes place for periods of up to 6.5 months (Dawbin, 1966). Many whales remain for a lesser period of about 4 months (IWC, 1979a). Juveniles migrate, but timing is slightly different than that of adults and penetration into high latitudes is not as great (Mackintosh and Wheeler, 1929; Kawamura, 1974; Lockyer, 1981a; Lockyer and Brown, 1981). Whereas sperm whales also undertake an annual feeding migration, the migratory status of the other southern odontocetes is poorly known. Estimated swimming speeds for southern cetaceans are presented in Table 37.

Blue whales

Blue whales have a circumpolar distribution. The distance covered annually on a round trip migration between 20°S and 65°S may be 9,000 - 11,000 km (Lockyer, 1981a). The arrival of blue whales in the Antarctic commences early in November, before fin, sei, and minke

Table 37. Comparative ranges of swimming speeds in Cetacea. (From Lockyer, 1981 a).

Species of Whale	Swimming speeds km/hr		
	Feeding	Migration and cruising	Maximum when alarmed
Blue	2-5.5	5-33	48
Fin	2-6.5	5-30	41
Sei	2-6.5	5-30	
Bryde	2-6.5	5-30	
Humpback	2-4	5-15	27
Minke	2-6	5-26	
Right	2-4	5-11	16
Gray	2-4	4- 7.5	16
Sperm		5-12	26
Killer		14-22	37
Dolphins		16.5-24	

whales. Adults arrive first, followed by juveniles about one month later, although there are semi-continuous migratory waves of arrivals. Pregnant females frequently are the first to arrive and last to leave. Lactating cows with calves are usually the latest arrivals (Mackintosh and Wheeler, 1929; Lockyer, 1981a). The whales depart in the same order of their arrival, excepting pregnant females. The average stay is about 4 months, so that most blue whales have left the Antarctic by March - April. Blue whales penetrate as far south as the ice-edge (Kemp and Bennett, 1932). Their departure from high latitudes may be hastened by the advance of the ice edge as winter approaches, physically excluding whales from the area.

Pygmy blue whales

Pygmy blue whales are found mainly around Marion Island, Iles Crozet and Iles Kerguelen (Ichihara, 1966b). The distribution is mostly sub-Antarctic, occurring in a restricted zone between 40°S and 55°S and 0° - 80°E (mainly Area III in the southern Indian ocean) (Mackintosh, 1965; Ichihara, 1966b). There are winter and early spring records in sub-tropical South African and West Australian waters (Chittleborough, 1963; Gambell, 1964). However, Zemsky and Boronin (1964) suggested that the subspecies remains within the same region throughout the year, with only slight north to south movements. Ichihara (1966) noted a possible seasonal migration on the basis of a mark recovery at 44°S on 4 April 1963 from a whale marked at 56°S on 1 December 1962. Aguayo (1974) reported pygmy blue whales at 33°S off Chile.

Fin whales

Gunther (1949) described a uniform circumpolar dispersion of fin whales throughout their Antarctic feeding grounds. The main concentrations are found where Antarctic krill are abundant (chiefly Areas II and III) (Mackintosh, 1965, 1973; Lockyer and Brown, 1981). The annual migration of fin whales is thought to be similar to that of blue whales (Lockyer and Brown, 1981; Brown and Lockyer, 1984). The sequence of arrival in the Antarctic varies by different age/sex classes and animals of different reproductive status (Mackintosh and Wheeler, 1929; Lockyer, 1981a).

Although the first fin whale migrants pentrate the Antarctic from October - November onwards, the peak presence of this species probably occurs about 2 - 3 weeks later than blue whales (Lockyer, 1981a) (this information is derived from catch data and may be slightly biased by preferential selection for blue whales). Most adult fin whales arrive in Antarctic waters about 3 weeks before the juveniles and depart by May. Rayner (1940) and Brown (1954, 1959, 1960, 1961, 1962b,c, 1966a,b, 1977a) showed that migration occurs between 20°S and 65°S within a few months. Brown (1954) demonstrated that longitudinal dispersion from mark to recovery was usually limited to 50 degrees either side of the original point of marking. Fin whales do not generally migrate as far south as the blue whales (Harmer, 1931; Kemp and Bennet, 1932).

Sei whales

Omura (1973) and Budylenko (1978a) suggested that several southern hemisphere populations of sei whales exist. Whales are segregated by age, size, and maturity by latitude (Doi, Ohsumi and Nemoto, 1967; Lockyer, 1977b) with mean size increasing with higher latitude. Doi et al. (1967) suggested that most sei whales remain north of 50°S year-round (this species apparently prefers a more sub-Antarctic habitat).

Group size while on the feeding grounds usually varies between solitary animals and 10+ individuals, with usual numbers in the range of 1 - 4 individuals (Lockyer, 1977b; Joyce, pers. comm.). Swimming speeds are 2 - 6.5 km/hr when feeding, and 5 - 30 km/hr when migrating (Lockyer, 1981a). Brown (1977b) demonstrated from marking data that migration occurs between South American, South African, Australian, and Antarctic waters. Timing of arrival is later than blue and fin whales, with peak arrivals in January, departures in April (Gambell, 1968).

Minke whales

Minke whales have a circumpolar distribution and inhabit areas close to the ice edge (Ohsumi, 1976). Sightings indicate high densities of minke whales in the Atlantic, Indian and South-west Pacific sectors (Arsenev, 1960; Ohsumi et al., 1970). Doroshenko (1979) suggested that in low latitudes four populations are evident: "Brazilian", "Indian", "New Zealand" and "Chile-Peruvian". Biochemical studies on genetic typing have indicated differences between minke whales in Areas IV and V but elsewhere differences are insignificant (Wada and Numachi, 1979; IWC, 1981).

There is some indication of north-south seasonal migrations in minke whales. Ohsumi (1973) recorded a marlin (Makaira sp.) spear from the tropics recovered from a minke whale caught at 64°S in January. Both Best (1974a, 1982) and Williamson (1975) recorded the presence of minke whales in low latitudes in winter and spring. Minke whales are present off the Brazilian coast in late spring, where they are reportedly hunted (Joyce, pers. comm.). Taylor (1957) recorded presumably accidental over-wintering by minke whales trapped in open water areas in the Antarctic ice pack.

School composition of minke whales is highly variable. In low latitudes, solitary and small groups of 2 - 5 whales have been observed (Budylenko and Pervushin, 1972; Williamson, 1975; Best, 1982). Ohsumi et al. (1970) found that aggregations seemed to increase with latitude, suggesting group feeding. Nevertheless, while single minke whales are common, groups of 10 - 25 are not uncommon, and aggregations as large as 90 have been observed (Joyce, pers. comm.).

Humpback whales

Like the blue and fin whales, southern "populations" of humpback whales are circumpolar and have been divided into six groups: 1) east coast of South America, 2) west coast of South America, 3) east coast of Africa, 4) west coast of Africa, 5) east coast of Australia and islands of the southwest Pacific Ocean, and 6) west coast of Australia. In summer, these groups migrate into five areas in the Antarctic: the southeast Pacific Ocean, south Atlantic Ocean, south of South Africa, southeast Indian Ocean, and south of New Zealand (Dawbin, 1966).

Long distance annual migration of humpback whales, which are often found closer to coasts than other species, occurs between the winter breeding grounds in the tropics and the summer feeding grounds in the Antarctic. Humpback whales are slightly slower than other rorquals, swimming at 2 - 4 km/hr when feeding and 5 -15 km/hr when migrating (Dawbin, 1966; Lockyer, 1981a). The southward spring migration is a procession led by newly pregnant females, followed by mature males, lactating females, and calves. While feeding in the Antarctic, the whales are dispersed. The northward migration generally follows the reverse of the arrival sequence, (i.e., lactating cows and calves lead, with the pregnant females last to depart). This latter group may stay south of 60°S from late November to May (6.5 months); most whales stay 5.5 months, and some for far less (Dawbin, 1966).

Right whales

Kawamura (1978) described distributions of whaling grounds for right whales in the southern hemisphere, based on Townsend's (1935) data. The distribution is virtually circumpolar, with heavy exploitation often near land masses. Most of these whaling operations were between 30°S and 50°S, north of the Antarctic Convergence. While right whales have been taken off South Georgia, the South Shetland Islands, and Graham Land (Hinton, 1925), it is probably correct to assume that today most animals remain outside the Antarctic. No direct evidence is available for separate stocks of right whales but distribution in winter suggests possible stocks on each side of the South Atlantic, Indian, and South Pacific Oceans. Breeding populations are currently being investigated off Patagonia (Mermoz, 1980) and South Africa (Best, 1981).

Maury (1852) analyzed monthly abundance of right whales by latitude between 0° and 50°E from 20°S - 50°S. The peak abundance for different latitudes was: (40°S - 50°S) December to May; (20°S - 30°S) May to July; and (30° - 35°S) July to December. These data suggest a possible migration. Best (1981) confirmed that off Hermanus, South Africa, (34°30'S), peak abundance occurred from August to November. However, Cawthorn (1978) reported slightly different behavior in the southwest Pacific. Right whales apparently bred in winter off Campbell Island (52°30'S, 169°10'E) and migrated north in spring and summer returning south in autumn.

Sperm whales

Sperm whales occur world-wide, but only the older males penetrate far south into the Antarctic (Best, 1974b; Lockyer and Brown, 1981). Females and juveniles reside permanently in waters north of 45°S (Best, 1974a). Neither the activities nor duration of the stay by males in the Antarctic are well documented. Movements of bulls from the Antarctic into temperate water is evidenced by skin fouling by the Antarctic diatom Cocconeis ceticola (Best, 1969a). Additional evidence of migration comes from the presence of Antarctic squid beaks in of stomachs of sperm whales taken off South Africa (Clarke, 1972). A slight southerly migration in summer and northerly migration in winter of sperm whales is evident from the seasonal distributions of catches (Townsend, 1935). However, some adult male sperm whales may remain in tropical and equatorial regions year-round.

Other odontocetes

Brownell (1974), Brown et al. (1974), and Nishiwaki (1977) reviewed the distribution of toothed Cetacea other than sperm whales in the Antarctic. The distribution of Hyperoodon and Berardius appears to be circumpolar, occurring right up to the ice edge in summer. However, due to their similar appearances at a distance, identification is easily confused (Gianuca and Castello, 1976). Some individuals remain south during winter evidenced by sighting of specimens in pools in sea ice (Taylor, 1957) and observations at Halley Bay (75°S) (Laws, pers. comm. in Brown and Lockyer, 1984). McCann (1975) suggested north-south migrations in the southern hemisphere by Berardius arnuxii, but this has not been confirmed. If Antarctic populations are similar to their Arctic counterparts, sexual segregation may occur (Mitchell, 1975; Benjaminsen and Christensen, 1979; Ohsumi, 1983). Bottlenose whales generally occur in groups of 2 - 20 animals, although larger schools are observed. Sometimes only males (in the Arctic) aggregate in schools (Tomilin, 1967).

Killer whales are abundant in Antarctic waters where their distribution is frequently circumpolar (IWC, 1982) and seasonally related to potential prey (Voisin, 1972, 1976; Condy et al., 1978). Their frequent sightings may be due in part to their distinctive body shape and coloration, which preclude confusion with other species. Dense seasonal concentrations are found in coastal Antarctic waters and off South Georgia. Mikhalev et al. (1981) and IWC (1982) reported a possible seasonal migration from low latitudes in spring to high latitudes in summer.

Davies (1960), Brownell (1974), and Nishiwaki (1977) indicated that Globicephala has a general distribution throughout the Southern Ocean but is rarely seen. Nothing is known of social groupings of Globicephala in the Antarctic. Sergeant (1962) reported pelagic schools of 20 - 100 individuals off Newfoundland, and schools of 200 or more in strandings.

Goodall (1978) reported the distribution of Commerson's dolphin around Tierra del Fuego and to the south from strandings and incidental kills. In the Antarctic, it has been recorded from S. Georgia and Iles Kerguelen and these may be separate populations. Pelagic sightings have been recorded from the Drake Pasage (Aguayo, 1975). Phocoena dioptrica is chiefly sub-Antarctic in distribution (Baker, 1977), but has been recorded as far south as South Georgia (Brownell, 1974). Lagenorhynchus cruciger has a circumpolar distribution in temperate and Antarctic waters.

Abundance

Estimates of the past and current population sizes of Antarctic whales are presented in Table 38. Although these figures represent the best estimates possible at the present time, they are by no means definitive. Many of the calculated figures remain the subject of discussion, further evaluation, and revision. Whereas baleen whales once had a total biomass of approximately 47 million metric tons in the 1920's, they now constitute only about 10 million metric tons of biomass. This dramatic reduction in whale stocks was the result of heavy exploitation between the 1920s and 1960s. Blue, humpback, fin, and sei whales were sequentially depleted and are now protected from commercial exploitation in the southern hemisphere (IWC, 1983). Only the minke whale is still taken commercially, but this harvest and other commercial whaling may cease for at least five years at the end of 1985 (IWC, 1983)(Norway, Japan, and the Soviet Union have registered objections to the moratorium). Southern right whales were also depleted to extremely low levels due to whaling in the 19th century (Townsend, 1935). Estimates of selected population abundance by statistical area are given in Table 39.

Population estimates for sperm and killer whales are given in Tables 38 and 39. The abundance of most other Antarctic odontocete species is largely unknown. For example, Phocoena dioptrica is known to occur south of the Antarctic Convergence only from a few sightings or old records (Brown and Lockyer, 1984). In contrast, Lagenorhynchus cruciger and Ziphiids are sighted regularly on IWC/IDCR whale assessment cruises (Horwood, 1981; Best and Butterworth, 1982).

Reproduction

General patterns

Although a 2-year reproductive cycle is common for most baleen whales, the actual pregnancy rate varies from approximately 0.3 to 0.5 (Mizroch and York, 1982). Conception and birth occur on the winter grounds, gestation being about one year (Laws, 1959; Lockyer, in press). Minke whales can reproduce annually, but their pregnancy rate is about 0.8. Right whales may breed only once every 3 years (Lockyer, in press). In general, weaning of the calf occurs during the first southerly migration postpartum, while on the Antarctic feeding grounds.

Table 38. Estimates of past (prior to exploitation) and current southern hemisphere whale populations.

Species	Past (1000s)	Current (1000s)	Reference
Blue	150-210	8 a	Gambell (1976)
		4.5	Masaki, Yamamura (1978)
Pygmy Blue	10	5 a	Gambell (1976)
		7.4	Masaki, Yamamura (1978)
Fin		85.2	Chapman, Breiwick (1979)
	400 a	80.5 a	Chapman (1976)
		78.2-80.5	Table 39
Sei	63.9-113 a	11.4-20 a	IWC (1980)
	192.3 a	94.5 a	Chapman (1977)
Humpback	90-100		Chapman (1974)
		3	Gambell (1976)
		3.5	Masaki, Yamamura (1978)
Right	100-194		Yawamura (1978)
		3-4	Gambell (1976)
Minke	?	305.2 a	Gambell (1976)
		258.3	Table 39
Sperm b	170 a	71 a	IWC (1983)
Killer	?	145-225	IWC (1982)
		247	Table 39

a: Exploitable population (excludes pre-recruited juveniles)
b: Males only

Table 39. Recent population estimates for southern hemisphere stocks of recruited stocks of sei, fin, and minke whales and total stocks of killer whales by statistical area.

Area	Sei a	Fin b	Minke d	Killer e
I	1,600	7,000	25,617	26,500
II	600(9,200)	17,500	22,873	12,367
III	1,150	34,700	50,016	38,278
IV	5,700	7,400	53,303	16,399
V	2,000	2,700	66,666	136,500
VI	400	11,200(8,900c)	39,846	17,192
TOTALS	11,450 (20,050)	80,500 (78,200)	258,321	247,236

a: 1979 estimate from IWC (1980)
b: post-1970 estimates from Chapman (1976)
c: IWC (1981)
d: 1978-84 estimates from IWC (in press)
e: 1978-82 estimates for Areas I, VI from IWC (1982); Areas II-V from Hammond (1984)

Sexual maturation occurs at about the same age in both sexes, usually between ages of 5 and 14 years, dependent on population and species and year of observation. At sexual maturity, approximately 90% of the ultimate body length has been attained (Lockyer, 1984).

Blue whales

Females conceive in June - July in low latitudes and give birth 11 months later to a single calf (Mackintosh and Wheeler, 1929). Pregnant females thus benefit from summer feeding in high latitudes to nourish the fetus. A 2-year breeding cycle is common, allowing for an 11-month gestation (Laws, 1959), 7-month nursing, and 6-month resting or anestrous state. A portion of the females do not breed at the end of the second year; the pregnancy rate is generally less than 0.5. Ichihara (1966b) presented some evidence suggesting bimodal breeding seasons: one peak of conception in February - April, and another in November - January. Ichihara (1966b) reported a 0.27 - 0.36 proportion pregnant in the mature female catch (excluding lactating females), which may indicate a reproductive cycle of up to 3 years or more. Males exhibit a slight seasonal increase in testicular activity in the males (Mackintosh and Wheeler, 1929) is a further reflection of this aspect.

Fin whales

The breeding cycle of fin whales is similar to that of blue whales. Calves are suckled for about 7 months in warm, low latitude waters (Mackintosh and Wheeler, 1929; Ruud, 1937) before being weaned mainly during the summer months in Antarctic waters (Mackintosh, 1965). Both Mackintosh and Wheeler (1929) and Laws (1961) reported seasonal spermatogenic activity in fin whales during winter with a protracted period from April to August, peaking in May/June, close to the time of breeding.

Sei whales

Conception occurs in July on winter breeding grounds (Gambell, 1968). Gestation lasts about 11 - 11.5 months (Gambell, 1968; Lockyer, 1977a), with calving occurring in about June. Lactation lasts 6 months (Gambell, 1968). No seasonal male reproductive cycle has been observed; it is assumed that female estrus provides the seasonal control of conception (Gambell, 1968). The availability of food may influence the duration of the reproductive cycle, usually 2 years, by increasing the resting phase in years of low food abundance (Gambell, 1968).

Minke whales

Conception occurs between August and September in low latitudes (Best, 1982). Gestation lasts about 10 months culminating in birth between May and June (Ivashin and Mikhalev, 1978; Best, 1982). Calves are weaned at about 4 months (Best, 1982). The calving interval was thought to be about 14 months, but many lactating females have been found

to be ovulating (IWC, 1979b; Best, 1982). Hence, a new pregnancy may be occurring before the calf is weaned. Masaki (1979) believed the reproductive cycle lasted about one year, with an annual calving in most seasons. Because minke whales have a shorter calving interval than species such as fin whales (annual versus biannual calving), their populations may be able to respond to changes in the environment quicker than other whales.

Humpback whales

The reproductive cycle of humpback whales bears many similarities to that of the blue and fin whale, but also differs in some aspects such as length of lactation. Chittleborough (1965) estimated lactation to last nearly 11 months, the longest of any baleen whale. The cycle takes basically 2 years, but may frequently be annual or triennial (Lockyer, in press). Conception occurs in the winter months of July and August, and birth occurs in July or August after a 11.5 month gestation (Chittleborough, 1965). A similar pattern of seasonal timing, duration of pregnancy and lactation was found for North Pacific humpback whales (Nishiwaki, 1959). Males show seasonal changes in spermatogenesis and testis weight (Omura, 1953; Symons and Weston, 1958; Nishiwaki, 1959; Chittleborough, 1965).

Age-specific reproductive rates of baleen whales

Age-specific reproductive rates are an important source of information for analyses of population dynamics and require reliable methods for determining age. Age determination by means of ear plugs has been a widely used technique (Purves, 1955; Laws and Purves, 1956; Nishiwaki, 1957; Nishiwaki et al., 1958; Ohsumi, 1964; Ichihara, 1966a; Roe, 1967; Lockyer, 1972, 1974; Chittleborough, 1959, 1960, 1965). However, there are some unresolved problems concerning whether the growth layer deposition rate is 1 or 2 per year. There is also uncertainty as to how deposition rates change as individuals grow older. Physical maturity occurs at an age of about 25 - 30 years in most baleen whales (Lockyer, 1981a). Life spans of some species may extend to 90 years (Lockyer, pers. comm.), but few whales have attained such ages due to whaling pressure.

Various methods have been used to estimate age at maturity, all dependent on catch data with its inherent size and age distribution biases. In general, age at maturity is determined from (a) mean age of whales just mature, (b) age at which 50% of the catch is mature, and (c) the transition phase of earplugs (Lockyer, 1972, 1977a, 1979). This latter method gives a historical perspective and allows attempts to assess trends. None of the 3 methods is directly comparable, and all are subject to different biases, some of which cannot be identified. A recent workshop on the problems of determining the age at maturity in minke whales from ear plugs highlighted potential sources of error in estimates (IWC, in press). The age at attainment of sexual maturity has been estimated as approximately 5 years for blue whales (Lockyer, 1981a),

5 - 6 years for pygmy blue whales (Ichihara, 1966b), 6 - 12 years for fin whales (Lockyer, in press), 8 - 11 years in sei whales (Lockyer, 1974), and approximately 7 - 14 years in minke whales (Kato, 1983) depending upon area and season.

Pregnancy rates (the proportion of mature females in the catch that are pregnant, excluding lactating females) may have fluctuated in relation to exploitation. Laws (1961), Mackintosh (1942), and Gambell (1973) reported an increase in the proportion of pregnant females in the fin whale and blue whale catches between about 1930 and 1970 from about 0.30 to about 0.60. These estimates however, were not analyzed according to area, latitude, month, or national data compatability. Mizroch (1981a,b) and Mizroch and York (1982) analyzed the data used by Gambell (1973) and could find no evidence of a clear trend; however, considerable seasonal variation existed for which no explanation was available. Lockyer (pers. comm.) has recently investigated an apparent positive correlation between variation in seasonal body fat condition, food supply, and fecundity in fin whales off western Iceland. These studies have some bearing on analysis techniques for southern stocks.

Sperm whales

The sperm whale is polygynous (Best, 1979), breeding from August to March, with a mid-summer peak in temperate waters (Best, 1968; Gambell, 1972). Births occur in February or later, gestation being about 15 - 16 months (Best, 1968; Gambell, 1972). Calves are suckled for approximately 2 years (Gambell, 1972; Best, 1974a). Females become sexually mature at about 9 years, males at about 19 years (Bannister, 1969; Best, 1970, 1974b; Gambell, 1972; Lockyer, 1981b). Fertility appears to vary with age and may affect the 4 - 5 year reproductive cycle. There is little evidence of a seasonal male sexual cycle, although Best (1969b) reported histological evidence for seasonal variation in androgenic hormone activity.

In sub-tropical and temperate waters, sperm whales have a social organization of several schooling systems (Ohsumi, 1971). Generally, it is the matriarchal nursery and harem schools which are coherent from season to season. Juvenile schools and various adult and sub-adult male groupings are less stable. During the breeding season, an adult bull will temporarily associate with a harem school, serving perhaps 12 - 14 females (Ohsumi, 1971; Berzin, 1972).

Other odontocetes

Reproductive parameters for Hyperoodon and Berardius are completely unknown in Antarctica. In Hyperoodon ampullatus (a northern hemisphere species) the gestation period is about one year, lactation is about 5 - 7 months, and the reproductive cycle is about 2 years (Tomilin, 1967). In Berardius (northern hemisphere), the gestation period is 16 - 17 months (Kasuya, 1977; Ohsumi, 1984).

Female killer whales attain sexual maturity at 7 - 8 years. Males mature sexually at 10 - 16 years. Gestation is likely to be between 12 months (Tomilin, 1967) and 16 months (Nishiwaki and Handa, 1958). Conception may occur in summer (January) in the Antarctic with birth approximately in autumn (IWC, 1982).

The gestation period in Globicephala off Newfoundland is about 15.5 months. Calves suckle for 6 - 9 months, although nursing may continue for up to 2 years (Sergeant, 1962). Similar to sperm whales, pilot whales are polygynous and have a harem schooling structure. Kasuya and Marsh (in press) recently reported an unusual occurrence of "wet-nurses" among reproductively elderly females in schools of G. macrorhynchus, which suggests a complex social structure within schools.

Goodall (1978) described a near term fetus of 73.4 cm from a Commerson's dolphin. She estimated birth to occur in early summer. The mother of the fetus was 8 years old and all vertebral epiphyses were fused, indicating both sexual and physical maturity.

Food Habits

A generalized diagram of the importance of principal prey of Antarctic whales is presented in Figure 30 (Laws, 1977b). Rough estimates of the amounts of prey consumed by current whale stocks are given in Table 40.

Blue whales

According to the classification by Nemoto (1959), the blue whale is a "swallower" type of feeder -- a volume of water and zooplankton is gulped and filtered through the baleen plates by means of internal pressure from tongue expansion. This type of feeding was further explained by Lambertson (1983). A major prey of blue whales is Antarctic krill (Mackintosh, 1942; Marr, 1956). In the sub-Antarctic, E. vallentini is an important food source (Nemoto, 1962; Doi et al., 1967; Kawamura, 1974). A daily intake of 30-40 g/kg of body weight was estimated for an average 120 day stay in Antarctic waters (Lockyer, 1981a). The first stomach (which is three-chambered) reportedly holds 1,000 kg (Zenkovich, 1969). It may not be unreasonable to assume a daily intake of about 4,000 kg for a fully adult blue whale (Lockyer, 1981a). Successful feeding probably is dependent upon locating high density swarms.

Blue whales arrive in the Antarctic in spring in a lean body condition and quickly fatten over 4 or more months. Body weight has been estimated to increase at least 50% for blue whales and over 30% for fin whales during the feeding season (Lockyer, 1981a). This fattening phenomenon is well documented from studies of increasing blubber fat thickness and commercial oil yield as the season progresses (Mackintosh and Wheeler, 1929; Lockyer, 1981a). These energy reserves are utilized chiefly during the winter when feeding may be as low as one tenth of the daily summer consumption (Lockyer, 1981a) (Fig. 31).

Fig. 30. Pie diagrams indicating food consumption of whales in the Southern Ocean. (After Laws, 1977b).

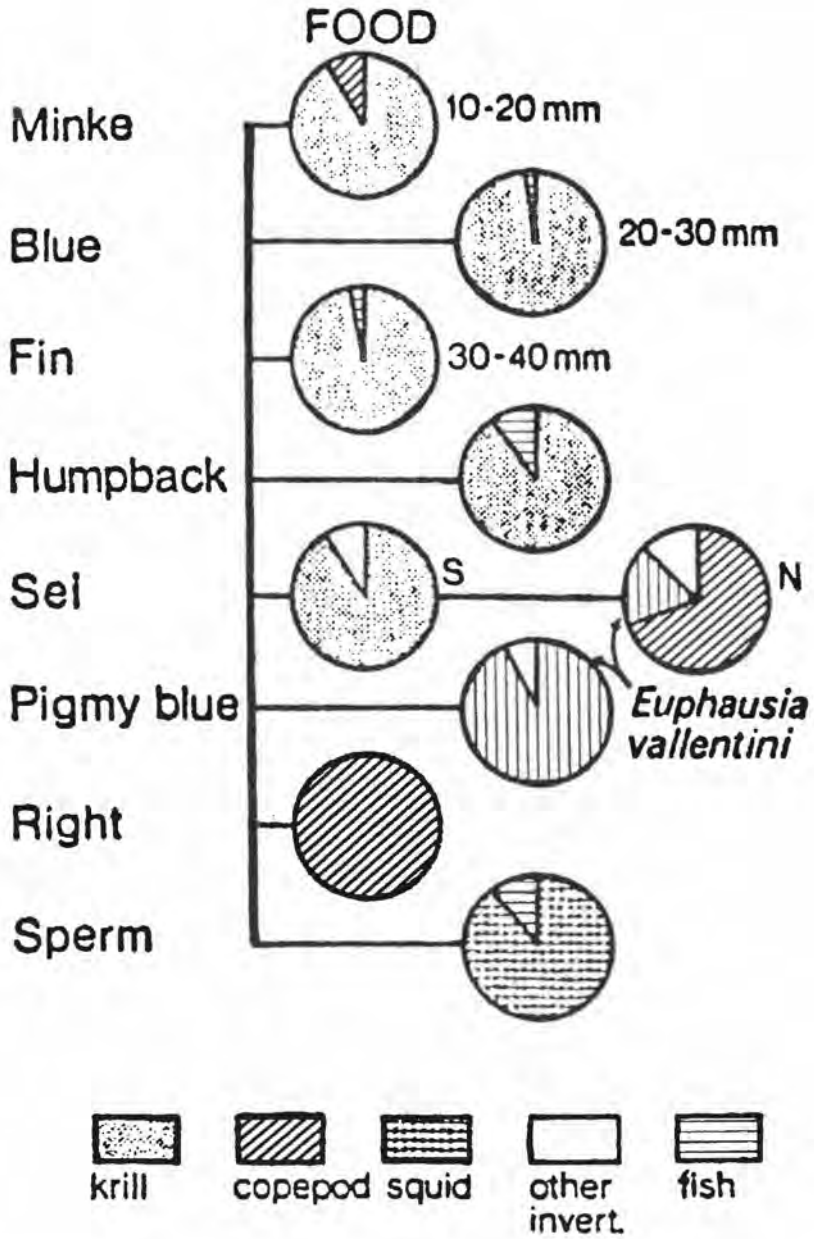
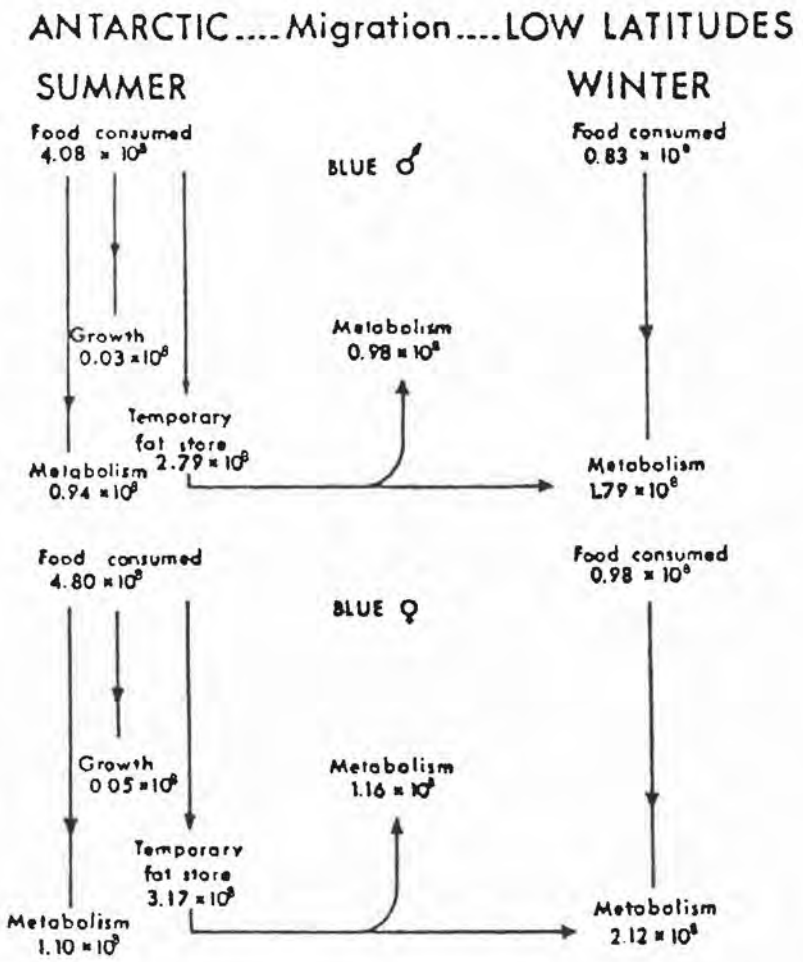


Table 40. Rough estimates of the current biomass of southern whale populations and food consumption in the Antarctic. Data from Laws (1977b), IWC (1979), and Tables 38 and 39 (this volume). Whales were assumed to consume prey daily amounting to a percentage of their body weight: 5% for humpback and juvenile fin whales, 3.5% for sperm whales (Lockyer, 1981b), and 4% for all others. All whales were assumed to actively feed in Antarctic waters 120 days per year (100 days for sei whales). Only one third of the male sperm whale population was assumed to feed south of the Antarctic Convergence. Although in this table all mature sei whales were assumed to spend some time south of the Antarctic Convergence, it is unclear what proportion venture there to feed, and what proportion remain farther north, where most exploitation has taken place. The units mt indicate metric tons.

Species	Stock size ($\times 10^3$)	Mean wt (mt)	Antarctic biomass ($\times 10^3$ mt)	Individual consumption		Annual food consumption of stocks (millions of metric tons)				
				Mt/ day	Mt/ year	Euphausiids	Cephalopods	Other Invertebrates	Fish	Total
Blue (all)	4.5	62.0	279	2.48	298	1.30	---	---	.04	1.34
Pygmy blue (all)	7.4	56.6	419	2.26	271	1.94	---	---	.05	1.99
Fin (mature)	84.0	48.0	4032	1.92	230	18.74	---	---	.61	19.35
Fin (juvenile)	42.0	10.0	420	.50	60	2.44	---	---	.08	2.52
Sei (mature)	16.0	17.5	280	0.70	70	1.01	---	.11	---	1.12
Humpback (all)	3.5	22.0	77	1.10	132	.42	---	---	.04	.46
Minke (mature)	258.3	7.0	1808	0.28	34	8.52	---	.26	---	8.78
Sperm (mature)	71.0	27.0	639	.94	113	---	2.41	---	.26	2.67
All	486.7	250.1	7949	---	---	34.37	2.41	.37	1.08	38.23

Fig. 31. Example of possible energy pathways in adult blue whales. (From Lockyer, 1981a).



Pygmy blue whales

Nemoto (1968, 1970) and Kawamura (1980) both classify the pygmy blue whale as a "swallowing" type feeder with a preference for euphausiids. Like the blue whale, its diet is more specialized than other rorquals. South of the Antarctic Convergence, Antarctic krill is the main prey, while species such as E. vallentini are taken in Kerguelen/Crozet Island waters (Nemoto, 1962). Pervushin (1968) recorded finding Myctophum punctatum and the cephalopod Onychoteuthis banksii in stomachs of pygmy blue whales from Crozet.

Fin whales

The fin whale is also classified as a "swallower" (Nemoto, 1959), and feeds primarily on euphausiids. In low latitudes during winter, fin whales sometimes feed opportunistically on shoaling fish and amphipods (Nemoto, 1970; Kawamura, 1974, 1980). Copepods (Kawamura, 1980) and squid (Peters, 1938) are also taken occasionally. Euphausiids (chiefly E. superba) comprised the diet in 99.4% of all fin whales examined in Antarctic catches from 1961 to 1965 (Nemoto, 1970). Other important components included: Euphausiacea -- E. vallentini, E. similis (sub-Antarctic), Thysanoessa macrura; Amphipoda -- Parathemisto gaudichaudi; Decapoda -- Munida gregaria (sub-Antarctic); Pisces -- Notolepis coatsi (Kawamura, 1980).

The quantities of prey consumed by fin whales are probably very similar to those consumed by blue whales (i.e., 30 - 40 g per kg body weight per day) during 120 days in the Antarctic. The first stomachs of fin whales, 18 - 23 m in length, have been reported to hold up to 900 kg (Sal'nikov, 1953; Kawamura, 1970, 1974). A daily intake of 2,000 - 2,500 kg of krill was estimated for adult fin whales (Lockyer, 1981a). Feeding is thought to be most active in the morning and early evening (Nemoto, 1959).

Sei whales

Nemoto (1959) described the sei whale as potentially both a "swallower" and a "skimmer" in feeding habits. Sei whales are opportunists able to skim small dispersed plankton like right whales, yet also take larger organisms from densely shoaling euphausiids or fish (Kawamura, 1974). Sei whales may have been limited by the presence of larger blue, fin, humpback, and right whales (Kawamura, 1978), until depletion of these stocks reduced feeding competition. Changes in the behavior and timing of sei whale arrival in Antarctic waters have been reported since the decline in other baleen whale stocks (Nemoto, 1962; Bannister and Gambell, 1965). These changes may indicate a response to a reduction in inter-specific competition.

Food items taken by sei whales in the Antarctic were thoroughly investigated by Kawamura (1970, 1974). South of the Antarctic

Convergence, E. superba is the staple (Matthews, 1938; Brown, 1968). In the sub-Antarctic, the following are locally important; E. vallentini, Parathemisto gaudichaudi, Calanus tonsus, and Calanus simillimus. Fish taken include Scomberisox saurus and Vinciguerria attenuuata, although other species encountered are consumed incidentally while feeding on planktonic prey. Other euphausiids taken include E. lucens, E. diomedeae, E. similis, Thysanoessa gregaria, and T. vicina. The copepods Clausocalanus laticeps and Drepanopus pectinatus are also taken.

Minke whales

Kawamura (1980) reported that stomachs from minke whales taken between 1961 and 1965 in the Antarctic contained euphausiids exclusively. Similarly, Ohsumi (1979) and Kawamura and Kikuno (1980) concluded that Euphausia superba was the sole food of minke whales in the Antarctic. Occurrences of other species such as Thysanoessa macrura were rare and perhaps incidental (Kawamura and Kikuno, 1980). Outside the Antarctic, minke whales eat other species such as E. vallentini (Kawamura, 1980).

Ohsumi (1979) assumed a feeding rate of about 4% body weight daily for the Antarctic minke whale. He observed that stomachs full of Antarctic krill weighed up to 136.4 kg. On that basis, minke whales would need to consume approximately 2 meals daily to meet energy needs. Ohsumi (1979) noted that although feeding took place throughout daylight hours, peak feeding occurred at dawn. A secondary peak may occur in evening (Ohsumi et al., 1970). Minke whales are "swallowers" in Nemoto's (1959) classification of feeding strategies.

Humpback whales

Humpback whales prey primarily on euphausiids, and were classified as "swallowers" by Nemoto (1959). Kawamura (1980) noted that gregarious fish are equally popular in the diet if abundant, as well as some demersal fish and various Crustacea. Nemoto (1970) reported only euphausiids from stomachs of humpback whales taken in the Antarctic between 1961 and 1965.

Quantities eaten by humpback whales have been assumed similar to those eaten by blue and fin whales during a 4 - 6.5 month stay in Antarctic waters (Lockyer, 1981a). Zenkovich (1969) estimated that an adult humpback whale might consume 2,200 kg krill daily and a full stomach might hold about 500 kg. However, Sergeant's (1969) hypothesis for northern populations) of 3 - 4% body weight required per day suggests that a daily rate of about 1,000 kg is probably more likely. Lockyer (1981a) calculated that by the end of the summer feeding period, a humpback whale may have doubled its lean, arrival body weight.

Right whales

Right whales were classified as "skimmers" by Nemoto (1959, 1968, 1970). The rostrum is narrower and more arched than in rorquals, the

grooves in the mouth and throat region that permit distension are absent, and the baleen plates are much longer than in blue and fin whales. The extremely fine baleen fringes enable right whales to filter organisms smaller than Euphausiids. "Skimmers" swim along open-mouthed. The density of prey is not as critical in this method of feeding, which is much closer to the usual notion of filter-feeding. Prey are retained in the oral cavity by the long baleen fringes as water flows through and out. Nemoto considered this type of feeding to be suitable for prey such as copepods and amphipods, although euphausiids would be taken if locally abundant.

Kawamura (1978) identified E. superba as the chief food of right whales in the Antarctic, although Munida gregaria is taken off S. Georgia, in sub-Antarctic waters off Patagonia, and possibly off New Zealand. Outside the Antarctic, the right whale probably takes mostly the copepod Calanus by analogy with its northern hemisphere counterpart (Kawamura, 1978). Kawamura (1978) found a coincident distribution between right and sei whales and Calanus tonsus between 30°S and 40°S during the austral summer. The main prey in these latitudes included copepods, amphipods, and E. vallentini.

Sperm whales

The principal component of the sperm whale diet throughout the world's oceans is cephalopods (Berzin, 1972; M. Clarke, 1983). Because of the sperm whale's deep diving ability, down to depths of 1,200 meters (Lockyer, 1977d) and from indirect evidence, to 3,200 meters (Clarke, 1972), is able to feed on a wide variety of cephalopod species. Many of its prey are known only from specimens retrieved from sperm whale stomachs (M. Clarke, 1980). Squid and fish are taken in the approximate ratio of 9:1. Kawakami (1980) presents a full review of data concerning the feeding habits of sperm whales worldwide. Cephalopod species taken by sperm whales are discussed further in Chapter 4. The most commonly taken species include members of the families Cranchiidae and Onychoteuthidae (Berzin, 1972; M. Clarke, 1983).

Fish are apparently taken opportunistically. Remains of Dissostichus mawsoni 120 - 140 cm long (up to 170 cm and 74 kg) were frequently found in stomachs of whales taken near the Balleny Islands (Berzin, 1972). Zemskii (1962) reported Notothenid fish up to 150 cm in length in sperm whale stomachs. Dissostichus eleginitides (70 - 138 cm and up to 44 kg) was reported by Korabel'nikov (1956) and Solyanik (1963) in the stomachs of sperm whales taken near Tierra del Fuego. Additional fish taken by sperm whales in the Southern hemisphere include Micromesistius australis and Ceratias holbochi (Koralbel'nikov, 1959). Large rays and bottom living sharks are occasionally taken as well (Clarke, 1972).

Feeding rates have been calculated as approximately 3% body weight daily in whales under 15,000 kg and up to 3.5% body weight daily in whales of 40,000 - 50,000 kg (Lockyer, 1981b). The first stomach would need to be filled 3 times daily for normal nourishment, while a nursing female might need to fill her stomach 4 - 5 times daily (Lockyer, 1981b).

Other odontocetes

Killer whales are important predators of marine mammals (whales, dolphins, and seals), birds (penguins), fish, and squid (Erickson and Hofman, 1974). In the Antarctic, the fish Dissostichus mawsoni is eaten as well as unspecified fish and squid. Larger items include adelie penguins, minke whales, crabeater seals, leopard seals, and southern elephant seals. Condy et al. (1978) found a seasonal correlation between distribution of killer whales and elephant seals near Marion Island. Cooperative hunting of crabeater seals by killer whales has been observed (Smith et al., 1981). Quantities of food consumed are likely to be about 4% body weight (Sergeant, 1969). No seasonal variation in levels of feeding have been documented, although diet composition may vary. The killer whale is usually present in cohesive family groups or pods. In the Antarctic, amalgamation of pods during feeding sometimes results in schools of 100 - 400 individuals (Doroshenko, 1978; Budylenko, 1981; Aubrey et al., 1982; Joyce, pers. comm.).

Sergeant (1962) described the preferred prey of Globicephala off Newfoundland as the squid, Illex illecebrosus, with which its distribution has been closely correlated. Squid may also be important for Globicephala in the Antarctic. Sergeant (1969) calculated a daily feeding rate of 4 - 6% body weight daily for adult pilot whales in the Arctic. The diet of Berardius and Hyperoodon is probably similar to that of sperm whales (Gaskin, 1976); in the Arctic these two species dive to great depths for long duration (Tomilin, 1967).

Ecological Interactions

Commercial exploitation of the great whales of the southern hemisphere had a major impact on the Antarctic marine ecosystem. There is evidence that groups such as seals and birds have been affected by harvest-related perturbations in recent decades (Bengtson, 1984). It is likely that less studied groups have been affected in ways not yet determined. The manner in which current whale stocks are being affected by altered abundance and behavior of its prey and competitors remains unknown. Increased populations of krill consumers such as crabeater seals and some penguin populations, as well as increasing pressure from commercial fisheries, may very well slow a recovery of whale stocks by altering the availability of krill.

The baleen whales rely heavily on Antarctic krill unless opportunistically presented with other locally abundant species such as E. vallentini (Nemoto, 1959, 1968; Kawamura, 1980). These whales undertake regular migrations (Lockyer and Brown, 1981), which means that other feeding areas may be available to them if food becomes locally scarce. The toothed whales are not direct consumers of krill, but may be linked to krill indirectly by eating krill consumers such as squid. Killer whales, which have a catholic diet (IWC, 1982), are unlikely to suffer initially from changes in krill availability although their diet

does include many species known to consume krill directly such as penguins and crabeater seals (Condy et al., 1978).

The International Whaling Commission has attempted on several occasions to predict the potential course and schedule of recovery of depleted whale stocks. Hypothesized time scales are in terms of many decades for recovery, not to pre-exploited population levels, but to a maximum sustainable yield level, generally assumed to be about 60% of the maximum size (see Allen, 1980). To date, evidence of recovery for blue, humpback, and right whales is limited, although small groups of right whales in specific localities appear to be growing at a steady rate (Best, 1981). Given the degree to which whale populations were reduced, it is likely that any potential recovery will take many decades.

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